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THE FRESHWATER REQUIREMENTS OF ESTUARINE PLANTS INCORPORATING THE DEVELOPMENT OF AN ESTUARINE DECISION SUPPORT SYSTEM

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UNIVERSITY OF PORT ELIZABETH

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THE FRESHWATER REQUIREMENTS OF ESTUARINE PLANTS INCORPORATING THE DEVELOPMENT OF AN ESTUARINE DECISION SUPPORT SYSTEM

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by

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1. GENERAL INTRODUCTION

What would a pristine estuary look like? Although this is impossible to say, it is obvious that there would be no discharge of domestic or industrial effluent into the system. Also, development within a few hundred metres of the banks would be absent as would dams in the catchment area. Given these conditions a wide range of natural ecological states are possible. Some of these might be desirable from a human point of view in that they may: be suitable as nursery areas for marine fish species; support a high biomass of adult fish of species preferred by anglers; have clean water and a low weed biomass, making them suitable for recreational swimming, boating and boarding; be attractive to migrant and resident bird populations and thus have value as a nature reserve; support a high biomass of benthic fauna of the species used by bait collectors. Truly pristine estuaries may or may not have these qualities. Equally these qualities are not necessarily incompatible with the various forms of human development.

The objective of this study was to assess how much and what pattern of freshwater input is required to achieve and maintain estuarine flora in a desirable state. The literature review describes the existing information relevant to this objective. Freshwater input to an estuary may not be the only factor affecting its ecological condition. Agricultural, industrial, urban and recreational developments and activities will also have an impact. Details of these effects are not included in this review.

From an ecological viewpoint the features which man may consider desirable in an estuary are often somewhat superficial in that they are dependent on the structure and productivity of the plant life in the estuary. The plant life in turn is controlled by the prevailing abiotic conditions, most of which are affected by freshwater inputs. Salinity is clearly and directly controlled by freshwater inputs. Estuarine nutrient levels will be determined by inflowing freshwater and also by tidal exchange with the sea which will depend on the status of the estuary mouth. This in turn will depend on maximum water velocities and sediment fluxes. Water velocities also affect water qualities and sediment characteristics such as aeration, turbidity, sediment particle size distributions and nutrient contents.

This review details existing information on the effects of the afore-mentioned abiotic factors on estuarine vegetation structure and productivity. Relevant information is also obtained from studies on freshwater wetlands, lakes and lagoons as plant communities in these systems also occur in estuaries. Estuarine vegetation has been divided into three groups, namely: macrophytes (vascular plants and macroalgae); planktonic microalgae (phytoplankton) and benthic microalgae. There is a chapter for each plant type and within each chapter both local and international literature is included. The final chapter includes literature on South African coastal water bodies, and in particular, Cape estuaries.

2. MACROPHYTES

Introduction

Estuarine macrophyte species composition, biomass and productivity, is determined by the complex interaction between numerous abiotic and biotic factors: irradiance, temperature, nutrient availability, grazing and competition. By the nature of their habitat, estuarine macrophytes are also subjected to varying salinities and fluctuating water levels. This section of the review focusses on the documented responses of estuarine macrophytes to varying levels of the aforementioned abiotic variables and puts particular emphasis where the variation is related to freshwater inflow. Typical estuarine macrophyte species and their productivities are also given for the readers convenience.

Estuarine macrophyte flora

For the purposes of this review, four functional ecological categories of estuarine macrophyte are recognised. Within each category different genera are typical of different salinity zones. We have followed the Venice system of classification for describing salinity ranges (Table 1; from Carriker 1967).

Table 1 Terms used to describe the different salinity zones.

Salinity (ppt)	Zone
0.5 - 5	oligohaline
5 - 18	mesohaline
18 - 30	polyhaline
30 - 40	euhaline
> 40	hypersaline

a) Floating macrophytes

The first group, the floating angiosperms, have aerial portions which are rarely submerged and roots which are submersed but not anchored in the sediment. These plants are generally restricted to the fresh and oligohaline sections of estuaries. They are also largely restricted to zones of quiet water, because populations can not build up in moving water.

Typical species include *Eichornia crassipes* (water hyacinth) and *Salvinia molesta*, both of which are exotic to South Africa and are regarded as nuisance weeds (Howard-Williams 1980, King *et al.* 1989).

b) Emergent macrophytes.

The emergent macrophytes are those plants which are rooted in soft intertidal or shallow subtidal substrata. However, they have photosynthetic aerial portions which are partially and/or periodically submersed. Typical species of freshwater and oligohaline zones are reeds, mostly *Phragmites* species, and rushes, mostly *Typha* species. Species of these genera (commonly *P. australis* and *T. latifolia*) dominate freshwater wetlands in temperate regions throughout the world (Simpson *et al.* 1983, Hocking 1989a), including South Africa (Day 1981a and b). They also fringe natural or man-made water bodies (Hocking 1989a, Howard-Williams 1980, Hecht 1973). *P. australis* is often associated with disturbed areas where the normal saltwater flushing has been arrested (Clark 1977, Lubke 1988). Unlike the other wetland genera it can tolerate salinities close to seawater and may fringe euhaline sections of estuaries or lagoons (eg. Christie 1981). However, groundwater seepage plays an important role in modifiying the salinity in such marginal reed beds. In this habitat *Phragmites* serves the valuable ecological function of protecting banks from erosion. *Phragmites*-dominated marshes are also considered a useful resource, not only because of their high productivity (Westlake 1963) but also, because they provide a habitat for many birds (Haslam 1971).

In meso-, poly- and euhaline zones, species of the grass *Spartina* are commonly found near the low water level, where they dominate extensive salt marsh areas. In some countries *Spartina* is considered valuable for salt hay farming and because it supports abundant wildlife (Roman *et al.* 1984). Higher up the shore, in poly- and euhaline zones, succulents such as *Salicornia* and *Sarcornia* spp., and sedges and rushes such as *Scirpus* and *Juncus* are common world-wide. In South Africa *Spartina maritima* is the only *Spartina* species found but there are several common *Sarcocornia* species: *S. pillansii*, *S. decumbens*, *S. perennis* and *S. natalensis*. Other South African salt marsh species include the small shrubs *Chenolea diffusa* and *Limonium scabrum*, as well as *Triglochin bulbosum* and *Cotula coronopifolia* (Day 1981a, O'Callaghan 1987). Even higher up, in the supratidal salt marsh areas, which are only occasionally inundated, one finds the grasses, *Sporobolus virginicus*, *Stenetophrum secundatum* and *Cynodon dactylum*, as well as *Juncus kraussii* and the succulents, *Disphyma crassifolium* and *Carpobrotus edulis* (Day 1981a, O'Callaghan 1987).

Salt marshes in South Africa have been reported to be of two main types. The first type, eg. Langebaan Lagoon, occurs potentially in estuaries where the tidal interchange predominates. These salt marshes are well-stratified with *Zostera capensis* at the low-water mark, followed by *Spartina maritima*. Above the *Spartina maritima* zone, *Sarcocornia perennis* is reported to appear, followed by *Triglochin striata* and occasionally, *Cotula coronopifolia*. The upper limits of the marsh area are indicated by *Limonium scabrum* and *Chenolea diffusa* (O'Callaghan 1987). The second type of salt marsh eg. Kleinmond Lagoon, is found in estuaries that are predominantly closed. In these salt marshes *Cotula coronopifolia* occurs at lower levels, followed by *Sporobolus virginicus*. *Juncus kraussii* is dominant in the upper levels with numerous herbs such as *Samolus porosus*, *Apium graveolens* and *Berula thunbergii* (O'Callaghan 1987).

c) Submerged macrophytes.

The submerged macrophytes are those angiosperms and seagrasses that are rooted in soft subtidal and low intertidal substrata. The plants' leaves and stems are completely submersed for most states of the tide.

In freshwater, oligo- and mesohaline waters, typical species world wide are *Potamogeton* spp., *Chara globularis*, *Elodea canadensis*, *Ceratophyllum* spp., *Myriophyllum alterniflorum* and *Ruppia* spp. (Haramis and Carter 1983, Collins *et al.* 1987). In South African brackish waters *Potamogeton pectinatus*, *Chara globularis* and *Ruppia cirrhosa* (=*spiralis*) are particularly common (Howard-Williams 1980, Bally *et al.* 1985). These macrophytes help to oxygenate the hypolimnion, anchor the sediment, increase the depth of the oxidized microzone at the sediment surface (thus reducing phosphate and ammonia release). Submerged macrophytes through the provision of a diversity of habitats, increase invertebrate and fish faunal diversity (Balls *et al.* 1989).

Although *Ruppia* spp. may tolerate high salinity, seagrasses dominate the lower intertidal and submerged vegetation of bays, lagoons and the poly- and euhaline sections of estuaries (eg. Lee and Olsen 1985, Howard-Williams and Liptrot 1980). Common genera world-wide are *Thalassia*, *Zostera*, *Halodule* and *Posidonia*. In Europe and America, *Z. marina* is the most extensively studied seagrass because of its abundance. In South Africa *Z. capensis* is the most abundant. *Halophila ovalis* often occurs in association with it but is seldom as abundant (Day 1981a).

d) Macroalgae.

The macroalgae make up the fourth category of estuarine macrophytes. These seaweeds may be intertidal (intermittently exposed) or subtidal (submerged at all times) and may be attached to hard or soft substrata, or they may be floating. Genera typically reported for estuaries are *Enteromorpha*, *Chaetomorpha*, *Cladophora* and *Ulva* (Lobban, Harrison and

Duncan 1985). *Codium*, *Ulva* and *Caulerpa* have been reported in South African estuaries (Day 1981a) and *Gracilaria verrucosa* has been found in lagoons and sheltered embayments (MacNae 1957, Christie 1981).

Although Christie (1981) found that *Gracilaria verrucosa* was the major primary producer in a South African lagoon, it is generally believed that macroalgae form a minor part of the estuarine flora. Day (1981a) states that "macroscopic algae are never abundant in coastal plain estuaries and are usually restricted to the cleaner rocks and man-made surfaces near the mouth". They are also not common in freshwater. Collins *et al.* (1987) found only two species of macroalgae out of a total of 38 submersed species in Lake George (USA).

Comparative productivities

On the basis of a between system comparison, the maximum standing biomass attained by emergent macrophytes is generally greater than that attained by other forms of estuarine macrophytes (Table 2). The same is true, on the whole, of productivity per unit area (Westlake 1963, Kennish 1986).

Comparing productivities within a brackish coastal lake system (Wilderness) in southern Africa, Howard-Williams (1980) found productivities (g dry mass m^{-2} y^{-1}) of the various macrophytes to be of the order: *Typha latifolia* > *Phragmites australis* > *Scirpus littoralis* (all emergents) > *Potamogeton pectinatus* > *Chara globularis* > *Ruppia cirrhosa* (all submerged).

However, in another southern African, brackish coastal lake and an associated estuary (Swartvlei), Howard-Williams and Allanson (1978 and 1979) found productivities (g C m^{-2} y^{-1}) of the major plant groups to be of the order: *Chara mariscus* > *Potamogeton pectinatus* (submerged) > *Phragmites australis* = *Scirpus littoralis* (emergent) > phytoplankton. In the coastal Langebaan lagoon, Christie (1981) found that the productivities of the more oligohaline emergents (*Phragmites* and *Typha*) and the salt marsh emergents (*Sarcocornia* and *Spartina*) were all similar. The salt marsh sedge (*Scirpus*) was about four times more productive and *Zostera* (submerged) only about a third as productive. The productivity of the red macroalga, *Gracilaria verrucosa* which was the dominant macrophyte, was slightly lower than that for *Spartina*.

Typical annual dry mass production for emergent macrophytes, both oligohaline and polyhaline species, is about 2500 g m^{-2} (Table 2). This is equivalent to 1250 g C m^{-2} y^{-1}, a carbon content of 45% being typical of these macrophytes. Although, on the whole, the poly- and euhaline species do not appear to differ in productivity from the oligo- and mesohaline species, it is notable that Ho (1979) estimated that *Phragmites australis* is

Table 2 Published biomass and annual productivities (dry mass) of various estuarine macrophytes. (Conditions: 1 = <18 ppt; 2 = 18-30 ppt; 3 = 30-40 ppt).

Biomass (g m^{-2})	Production (g m^{-2} y^{-1})	Genus & group	Ref.
<u>Floating macrophytes</u>			
566	-	Nuphar^{1}	(1)
<u>Emergent macrophytes</u>			
2800-9400	1000-3500	Typha^{1}	(1)
-	1249	Typha^{1}	(5)
-	1004	Scirpus^{1}	(5)
-	960	Scirpus^{1}	(8)
-	14945	Phragmites^{1}	(2)
-	930	Phragmites^{1}	(5)
1500	1621	Phragmites^{2}	(7)
-	1790	Phragmites^{2}	(8)
-	2318	Phragmites^{1}	(3)
-	3416	Juncus^{2}	(3)
648-1376	1501-6043	Spartina^{3}	(3)
<2400	700	Spartina^{3}	(4)
<u>Submerged macrophytes</u>			
-	231	Chara^{2}	(5)
150	263	Chara^{2}	(6)
-	2230	Chara^{2}	(8)
-	415	Potamogeton^{1}	(5)
1950	2506	Potamogeton^{2}	(6)
-	4124	Potamogeton^{2}	(8)
-	83	Ruppia^{2}	(5)
-	710	Ruppia^{2}	(8)
226	-	Zostera^{3}	(10)
<u>Macroalgae</u>			
132	-	Cladophora^{2}	(9)
543	-	Gracilaria^{3}	(10)

References:
1. Simpson *et al.* 1983
2. Hocking 1989a
3. Hopkinson *et al.* 1978
4. Mountford 1980
5. Howard-Williams 1980
6. Howard-Williams and Allanson 1978
7. Howard-Williams and Allanson 1981
8. Bally *et al.* 1985
9. Branch and Day 1984
10. Christie 1981

perhaps the most productive emergent macrophyte in temperate regions. Hocking (1989a) obtained an even higher value for *P. australis* growing in Australian swamps (Table 2). He speculates that this extremely high productivity is due to the mild winters, high irradiances and the nutrient enrichment in the swamp.

In general, there is considerable variation between systems (Kennish 1986 and Table 2). Most authors ascribe this to differences in environmental conditions. Howard-Williams (1980) found that the productivities of all the macrophyte groups in the Wilderness lakes, southern African, mentioned above, were low compared to those for the same species in other systems. He speculates that fluctuating and occasionally high salinities and possibly nutrient limitation are responsible. On the other hand, some of the variation may be due to differences in the methods used to estimate production.

The percentage contribution to total system primary production, by the different macrophyte groups, is even more variable, being primarily a function of topography. For example, in an oligohaline swamp in Canada, algal production contributes less than 1% to the productivity in such swamps. In contrast, in salt marshes, algae are found to contribute about 30% (Gallagher and Daiber 1974). Lee and Olsen (1985) found that, in USA coastal lagoons (salinity: 23-30 ppt), *Zostera marina* made up 50-80% of the macrophyte biomass and contributed over 50% to total primary production. Macroalgae and benthic microalgae contributed 40% and phytoplankton only 10%. In Swartvlei, a southern African brackish system, Howard-Williams and Allanson (1978 and 1979) found that because of their high productivities, *Potamogeton* and *Chara* (the two submerged macrophyte species), contributed 85% to the total production while the emergents contributed only 9%. The remainder was contributed by phytoplankton.

The balance between production and decomposition rates is important in determining sedimentation rates, particularly in systems where imports and exports of particulates are small. In natural systems, decomposition rates of macrophytes are generally high and often balance production. In a freshwater wetland dominated by emergent macrophytes, Simpson *et al.* (1983) found that 30% of the litter mass was lost within 30 days and that there was no litter present at the start of each growing season. In Swartvlei, Howard-Williams and Allanson (1978, 1979) found that despite extremely high productivities by submerged macrophytes, there was no build up of organic sediment due to the high decomposition rates which were experimentally verified. Decomposition rates do not appear to be affected by salinity. In comparing oligo- and polyhaline reaches of the same estuary, Hopkinson *et al.* (1976) found no significant differences in decomposition rates. Rates for all species (emergent macrophytes) were between 4.9 and 25.2 mg g^{-1} and averaged 10 mg g^{-1}.

Salinity related effects

The species composition of estuarine macrophyte communities varies with salinity. Typical species compositions for floating, emergent and submerged macrophyte communities of different salinity zones have been described above. This section gives more detail on specific salinity tolerances and salinity related changes in species composition in the field.

Water column salinity in which various estuarine macrophytes have been observed are given in Table 3. Although many references may be available for a single species, the references given in Table 3 are those that report the widest salinity ranges. These salinities do not necessarily reflect physiological limits or the duration for which extremes can be tolerated. However, they give some indication of salinity ranges in which the species are likely to be found. Species distribution will be determined not only by the salinity tolerances of the mature plants but also by competitive interactions and by the salinity tolerances for flowering and seed germination. Furthermore, nutrient availability, irradiance and temperature, may influence salinity tolerances. Salinity tolerances under fluctuating salinities may also differ from those under stable conditions.

Within marshes, sediment salinity plays an important role in determining the vertical and horizontal distribution of emergent macrophyte species. The sediment salinity is controlled by:

rainfall and evaporation on the marsh;
groundwater seepage from adjacent land;
the salinity of the tidal water that inundates the marsh.

The relative importance of these three factors depends on the location within the estuary (Haw 1984) and the climate. In arid areas, for example, most of the moisture for a marsh is provided by tidal flushing (Zedler 1980). Freshwater inflow into an estuary is important as it recharges groundwater sources and dilutes the tidal water that inundates the marsh. Lack of freshwater input into the Kromme estuary (southern Africa) has resulted in high water column salinity that has caused salt accumulation in the intertidal marshes (Adams *et al.* 1992).

The salinity of the surface sediments and pore water salinity are controlled by the salinity of the tidal water (Lindberg and Hariss 1973, Price *et al.* 1988). However, only persistant changes in salinity conditions of the estuary water are reflected in pore water salinities. Thus, for example, while some salt marshes in Louisiana (USA) may experience semi-diurnal fluctuations in water salinity of up to 10 ppt, sediment salinities are more stable (Hoese 1967). Pore water salinities near the sediment surface are controlled by density gradient induced exchange across the sediment-water interface.

Table 3 Published water column salinity ranges in which various estuarine macrophytes have been found.

Genus and species	Salinity (ppt)	Reference
Floating macrophytes		
Eichhornia crassipes	< 2.5	(1)
Myriophyllum spicatum	< 13.3	(1)
Salvinia molesta	< 4	(2)
Emergent macrophytes		
Phragmites australis	< 25	(3)
Scirpus maritimus	7-12	(4)
Scirpus maritimus	0.5-5	(5)
Salt marsh macrophytes		
Arthrocnemum australasicum	< 44	(6)
Suaeda australis	< 7	(6)
Triglochin striata	< 21	(6)
Juncus kraussii	< 15	(7)
Salicornia virginica	< 45	(8)
Spartina alterniflora	< 45	(9)
Sporobolus virginicus	< 30	(10)
Submerged macrophytes		
Chara mariscus	5-15	(11)
Potamogeton pectinatus	5-15	(11)
Potamogeton pectinatus	< 19	(12)
Ruppia cirrhosa	2-40	(13)
Ruppia cirrhosa	< 50	(12)
Ruppia maritima	2-18	(13)
Zostera capensis	5-40	(14)
Zostera capensis	< 45	(12)
Macroalgae		
Cladophora albida	2-50	(15)
Enteromorpha intestinalis	0-51	(16)

References:

1. Haller *et al*. 1974
2. Howard-Williams 1980
3. Starfield *et al*. 1989
4. Bally *et al*. 1985
5. Lubke and van Wijk 1988
6. Clarke and Hannon 1970
7. Heinsohn and Cunningham 1991
8. Pearcy and Ustin 1984
9. Linthurst and Seneca 1981
10. Breen *et al*. 1977
11. Howard-Williams and Liptrot 1980
12. Ward 1976
13. Verhoeven 1975
14. Day 1981a
15. Gordon *et al*. 1980
16. Reed and Russell 1979

At greater depths pore water salinities are influenced by the movement of the groundwater table (McKlusky 1968, Lindberg and Harriss 1973). The depth at which either mechanism predominates varies with the hydrology of the marsh. For example, Bolen (1964) found that sediment salt content decreased with sediment depth and frequency of inundation in a spring-fed salt marsh in western Utah, while in the coastal marshes of James Bay, salinity increased with depth because the high infiltration rates promoted leaching that reduced surface salinities (Price *et al.* 1988). Sediment characteristics such as permeability, porosity, compaction and grain size affect the rate of water exchange and therefore also affect the salinity (Lindberg and Harriss 1973). For example, Smart and Barko (1978) report that under conditions where the free water salinity of a silty clay was 32 ppt, that of a clay was only 18 ppt.

In reviewing the literature on salt marshes along the south Atlantic USA coast (Louisiana) Hoese (1967) found that salt marsh communities (usually dominated by *Spartina foliosa*) occurred where average water column salinities were between 10 and 30 ppt. However, they also occur where salinities seldom fall below 30 ppt; where waters become fresh at times; and where water column salinities exceed 40 ppt at times. They do not occur in areas where salinities persistently exceed 40 ppt.

Despite their general association with euhaline (30-40 ppt) conditions, it seems that high salinity is not physiological optimal for these species. Chapman (1960) has shown that few species will germinate at salinities greater than 20 ppt and Ungar (1962) found that germination in succulent halophytes dropped when the particular limits of salt tolerance were reached for each species. Both field and laboratory studies have also shown that the growth rates of many salt marsh species increase as salinity decreases (Phleger 1971, Smart and Barko 1978, Price *et al.* 1988). This generally seems to apply to species that have a low salinity range of tolerance, eg. *Sporobolus virginicus* (Breen *et al.* 1977), *Cyperus* and *Phragmites* (Millard and Broekhuysen 1970). However, even the more salt tolerant species such as *Spartina foliosa* show better growth in lower salinity under labortatory conditions (Phleger 1971).

Both field observations (Hoese 1967) and laboratory growth studies (Chapman 1960, Phleger 1971) indicate that even the most salt tolerant emergent macrophytes, such as *Spartina* spp. do not grow in salinities of 45 ppt. They can survive these conditions for short periods but not persistent salinities in excess of 40 ppt. Some authors believe that such hypersaline conditions would lead to barren salt pans (Allanson and Read 1987). Others have suggested that the removal of the macrophyte canopy and improved water clarity associated with the lack of fresh or marine water inflow could lead to increased phytoplankton and benthic macroalgal productivity (Hoese 1967).

Within the range 0-40 ppt, long term salinity changes in either direction lead ultimately to changes in the marsh community. For example, McKee and Mendelssohn (1989) found that freshwater emergent macrophytes succumbed to sudden (< 1 day) salinity increases of 15 ppt in magnitude but were replaced in the field by more salt tolerant species. Roman *et al.* (1984) found that numerous coastal salt marshes areas in USA have changed from *Spartina*-dominated systems to nearly monotypic stands of *Phragmites australis* following tidal restriction. This restriction of the normal tidal flushing may be caused by the construction of roads, bridges, causeways, impoundments or tide gates. In the north American estuaries, this restriction has resulted in: a reduction in the salinity both of the water column and the sediment; a lowering of the water table; and a reduction in the height of the upper marsh due to the drying and subsequent compaction of the marsh peat. Roman *et al.* (1984) regarded the reduction in salinity as the primary reason for the shift in the vegetation.

Responses are not always immediate. For example, Howard-Williams (1980) found that the distribution of macrophyte species in the shallow coastal Wilderness lakes did not relate to the average water salinities (5-13 ppt) at the time of the study. The least saline area had no *Typha latifolia* and no *Scirpus littoralis* although these are generally found in fresh or brackish water. In addition there was less *Chara globularis* and *Potamogeton pectinatus* (both fresh and brackish water species) in the less saline waters, whilst *Ruppia cirrhosa* and other more salt tolerant species decreased from brackish to saline water. Howard-Williams speculates that the vegetation distribution is a function, not only of the present but also past environmental conditions. The least saline lake (Wilderness Lagoon) is opened to the sea annually. At such times salinities reach 35 ppt in the lagoon but the remainder of the system stays brackish. This annual intrusion of saline water presumably prevents colonization by *T. latifolia* and *S. littoralis* but does not affect the *Phragmites australis* which grows equally well in an adjacent freshwater system. It has been reported that *Phragmites* has a wide range of ecotypes, some of which are salt tolerant (Bjork 1967, and Waisel and Rechav 1970, in Howard-Williams 1980).

The effects of decreasing salinities for various time periods has been studied by Zedler (1983). She found that a short-term (< 1 year) reduction in salinity, from 35 ppt to 14 ppt, in a *Spartina foliosa* dominated salt marsh (California, USA) lead to a 40% increase in productivity of that species. A similar decrease in salinity in a *Salicornia virginica* dominated marsh led to a 160% increase in productivity. An extreme reduction in salinity, from 35 ppt to 2-10 ppt, (due to flooding) which was subsequently maintained (by irrigation water inflows) led to mass mortality of the dominant, *Salicornia virginica*. Within 3 months the area was recolonized and dominated by *Typha* spp (bulrush). When salinities were reversed again, a year later, this vegetation died and was not recolonised by *Salicornia*. Zedler (1983) noted that this was not surprising in view of the limited ability of the native salt marsh species to invade new habitats. Consequently, such areas are susceptible to invasion by exotics.

If marsh salinity is reduced, halophyte growth will immediately improve. However, too much freshwater may eliminate the salt marsh community. Management for the maintenance of natural salt marsh communities must, therefore include management of the freshwater inputs, so that the timing and duration of freshwater discharge do not exceed the threshold for compositional change (Zedler 1983).

The submerged macrophytes, including the macroalgae, are affected primarily by water column salinity and may respond to fairly short term fluctuations. For example, Robinson *et al.* (1983) found that *Ruppia* dominated Smiths Lake during low salinity periods whereas *Zostera capricorni* and *Halophila ovalis* had a greater coverage during marine conditions. On the other hand, Howard-Williams (1980) found that *Potamogeton*, *Chara* and *Ruppia* did not respond to annual switches in the salinity gradient which occurred as a result of freshwater inputs at times when the mouth of the system was closed.

As mentioned above, competitive interactions may also be important in controlling apparent salinity tolerances in the field. In Swartvlei, a southern African estuary, Howard-Williams and Liptrot (1980) found that *Ruppia cirrhosa* occurred along the entire estuary but was densest where the salinity fluctuated around 20 ppt. This is despite the fact that *Ruppia* has a wide salinity range of tolerance that ranges from nonsaline to hypersaline conditions (McMillan 1974, Verhoeven 1975). Under experimental conditions *Ruppia* can withstand up to 74 ppt (McMillan and Moseley 1967) and of all the submerged angiosperms found in saline conditions only *Ruppia* can be maintained indefinitely in tap water. Howard-Williams and Liptrot (1980) speculated that the horizontal zonation of *R. cirrhosa* was maintained by competition with *Z. capensis* at the euhaline end (35 ppt) and *P. pectinatus* and *C. mariscus* at the fresh (10 ppt) end. Flowering in *Ruppia* is confined to low salinities and seed-set occurs at a salinity of 28 ppt or less (McMillan 1974). The distribution pattern may, therefore, reflect the salinity range for reproduction rather than that for vegetative growth. Howard-Williams and Liptrot (1980) also found that, although *P. pectinatus* and *Chara mariscus* were absent where salinities sporadically exceeded 10 ppt for short periods, a period of several months at 16 ppt had no deleterious effect on the established populations. This again implies, either that competitive interactions are operating, or that there are differences in the salinity tolerances for vegetative growth and reproduction.

Although there are many freshwater algae, brackish water macroalgae do not appear to have evolved. The macroalgae found in saline and brackish waters (> 10 ppt) are, therefore, primarily marine species (Lobban, Harrison and Duncan 1985). Intertidal marine seaweeds are generally able to tolerate salinity fluctuations of 10-100 ppt and subtidal species 18-52 ppt (Gessner and Schramm 1972). Species found in estuaries show lower and narrower tolerances. Reed and Russell (1979) found that certain genotypes of *Enteromorpha intestinalis* from intertidal pools and estuaries, could tolerate 0-51 ppt, while Gordon *et al.* found that *Cladophora aff. albida* in Peel Inlet in Australia tolerated an annual salinity range of 2-50 ppt. Other species, such as *Bangia*, despite narrow salinity tolerances, are found both at the head and the mouth of estuaries. It appears from acclimation experiments that such species achieve this apparent wide salinity range from a gradual acclimation process. Various descriptions of the penetration of macroalgae into estuaries show that, in general, the Chlorophyta (green algae) penetrate higher than the Rhodophyta (red algae) and Phaeophyta (brown algae). This pattern is generally ascribed to the salinity gradient but physiological data is scarce (Lobban, Duncan and Harrison 1985).

Nutrient related effects

Nutrients in estuaries are largely allochthonous most being brought down by the river from the catchment or more rarely being imported from the sea by tidal exchange (Hart and Allanson 1984, Kennish 1986). The original source of most nitrogen and phosphorous in estuaries is the weathering of rocks and leaching of soils on land (Day 1981c). However, at present, anthropogenic activity is a predominant source of nutrient elements in some systems. Increased sewage production, agricultural fertilization and urbanization have coincided with the accelerated inflow of nutrient elements in estuaries during the past two decades (Kennish 1986).

The addition of nutrients to the water column usually leads to increased macrophyte productivity. Blooms of the water hyacinth (*Eichornia crassipes*) have been noted periodically in nutrient loaded waters (King *et al.* 1989) and blooms of macroalgae, particularly species of *Ulva*, *Enteromorpha* and *Cladophora*, have long been associated with sewage effluents (Sawyer 1965, Johnston 1971, Sevell 1982 as cited by Josselyn and West 1985). Reduced freshwater input decreases flushing and dilution of wastes. The resultant decline in estuarine water quality can result in blooms of these nuisance algae.

Brackish water emergent macrophytes appear to have a large capacity for nutrient uptake via increased productivity. This was proved by the extremely high productivity of *Phragmites* in nutrient loaded Australian swamps (Hocking 1989a); and by using emergent macrophyte-dominated swamps as natural filters for sewage water (Sloey *et al.* 1978). However, while emergent reedswamp vegetation may reduce eutrophication by absorbing nitrogen and phosphate from inflowing polluted water (Mason and Bryant 1975), it is sometimes claimed to increase eutrophication following the release of nutrients during decomposition. Hocking (1989a and b) examined the seasonal dynamics of nutrients in *P. australis* in a nutrient-enriched, freshwater swamp in Australia, and found variable results for the different ions. Sulphur, magnesium, zinc and copper were transferred from shoots to roots during senescence with only 17-38% efficiencies. On the other hand, nitrogen, phosphorus and potassium were translocated from senescing shoots to below ground organs with 60% efficiency, and although some potassium, chloride and sodium were lost from leaves and stems by leaching, nitrogen leaching losses were less than 5%. Hocking concluded that emergent macrophytes are indeed a sink for nutrients not just a temporary seasonal store. This is in contrast to the conclusion reached by Simpson *et al.* (1983) who studied the distribution and movement of nitrogen and phosphorus in a freshwater, tidal marsh adjacent to the Delaware River (Louisiana, USA). They found that more than 80% of the nitrogen and phosphorus was leached from the aboveground parts of the freshwater perennial macrophytes (*Typha* spp. and *Nuphar advena*) during senescence, in fall. However, during the summer growing season these macrophytes retained all the inorganic nitrogen and phosphorus from the local sewage outfall. Simpson *et al.* concluded that the marsh is a sink for nutrients but only during the growing season.

In contrast to the fresh and brackish marshes, salt marshes are generally considered to depend on recycled nutrients rather than those carried in the freshwater input (Schelske and Odum 1961). However, most of these nutrient are derived from the muddy sediment and silt carried down in the rivers and deposited in the salt marsh areas. The incidence of anthropogenic nutrient loading of salt marshes appears to be uncommon.

Submerged macrophytes also possess an outstanding ability for assimilating nutrients and creating favourable conditions for microbial decomposition of organic matter (Nienhuis 1983). It is for this reason that submerged macrophytes have been used together with emergent reeds for wastewater treatment (Mitchell 1978). However, responses in unmanaged systems are not always consistent. In the Potomac River (USA), Haramis and Carter (1983) found that historically nutrient enrichment had led to a decrease in the biomass of submerged macrophytes (viz. *Potamogeton* spp., *Ruppia* spp., *Ceratophyllum* spp., *Chara* spp., *Elodea* spp. *Myriophyllum* spp.) and the disappearance of seagrasses from the more saline zones. They speculate that these effects are caused by the severe shading by phytoplankton blooms which occur in response to the nutrient loading. Similar results have been reported by Mitchell (1989). He found that phytoplankton and macrophytes predominated alternately in irregular cycles in a system with no anthropogenic nutrient loading. Mitchell (1989) proposed that phytoplankton blooms in response to the nutrients brought in with freshwater pulses, reduced irradiance levels. Consequently the submerged macrophytes died back, releasing their nutrients which were then taken up by the phytoplankton and filamentous algae. Eventually the phytoplankton would outgrow the nutrient supply, settle to the bottom and die, releasing their nutrients and allowing the submerged macrophytes to grow again. He suggests that nutrient enrichment disrupts this cycle, as the algal blooms do not die down.

Balls *et al.* (1989) found that experimental nutrient additions to shallow, macrophyte-dominated, freshwater ponds (England), did not give the predicted responses. Chlorophyll-*a* levels did not increase and the macrophytes did not disappear. Furthermore, Lukatelich *et al.* (1987) presents circumstantial evidence that nutrient loading has led to an increase in the biomass of the submerged macrophyte *Ruppia*, in an Australian estuary.

Some of the variablility in the response of the submerged macrophytes to nutrient loading may be related to the extent to which they can utilize water column nutrients. Carignan and Kalff (1980) found that the five common macrophytes growing in oligotrophic and mesotrophic waters took up all their phosphorus from the sediment. The same was found for potassium and nitrogen (Huebert and Gorham 1983, Nichols.and Keeney 1976, Toetz 1974). However estuarine submerged macrophytes such as *Zostera*, *Ruppia* and *Potamogeton* absorb nutrients through their roots and leaves (McRoy *et al.* 1972).

The variability in submerged macrophyte responses may also be related to sediment nutrient dynamics. Estuarine sediments contain large reservoirs of nutrients and can in particular act as a phosphorus sink (Howard-Williams and Allanson 1978). Although the sediment may be rich in nutrients diffusion of nutrients to the roots (and subsequent uptake) may not equal demand. Plants may therefore be nutrient limited even when growing in nutrient rich sediments (Orth 1977, Harlin and Thorne-Miller 1981). This was indicated by the stimulation of *Z. marina* growth when ammonia and phosphate were added to the seagrass bed (Harlin and Thorne-Miller 1981). Several other studies have also indicated that submerged macrophytes may be nutrient limited in which case positive responses to loading would be expected. Barko and Smart (1986), using laboratory trials, concluded that nitrogen and potassium limited submersed macrophyte biomass in some natural systems. The same authors (Barko 1982, Barko and Smart 1986) also found that production was positively related to sediment organic matter content. However, findings are not always consistent. For example, Anderson and Kalff (1988), examining the relationship between submersed aquatic macrophyte biomass and sediment characteristics (in temperate lakes in Canada) found no correlation between biomass and sediment ammonium or available phosphorus. However, sediments with higher potassium contents supported significantly higher biomasses. Also organic sediments supported significantly more biomass than gravel, and silt supported more than sand. In contrast, Anderson and Kalff (1986a) demonstrated, by *in situ* fertilization experiments, that *Myriophyllum spicatum* was limited by the availability of sediment nitrogen, and Anderson and Kalff (1986b) found significant correlations between submerged macrophyte biomass and sediment nitrogen, potassium and phosphorus.

It is important to note that correlations between sediment nutrients and macrophyte biomass do not necessarily indicate the causal relationship implied above. For example, in a system with underlying sediments of marine sand (with low nitrogen and phosphorus contents), Howard-Williams (1980) found a build up of organic matter and higher nitrogen and phosphorus contents at the sediment surface. He speculates that this build up of surface nutrients is the result rather than the cause of the macrophyte production. He suggests three possible mechanisms: i) continuous depletion of the lower sediments followed by surface deposition on death of the macrophytes; ii) physical trapping of nutrient rich detritus from water flowing through the macrophyte communities; and iii) nitrogen fixation. Howard-Williams (1980) ascribes the higher organic content of the sediment below the emergent (as compared to the submerged macrophytes) to the higher production rates and the slower decomposition rates of the former.

The balance between production and decomposition rates (particularly in systems with low flushing rates) is important, not only in determining nutrient accumulation but also, in determining the rate of sedimentation. Substantial rates of organic matter accumulation, together with inorganic sediment and allochthonous organic material deposition ultimately leads to a decrease in water depth and changes in the macrophyte communities. This is generally regarded as a natural process (Day 1981a). However, this process may be greatly accelerated by reductions in flushing and by increases in nutrient loading.

Sediment related effects

As indicated above, the nutrient status of the sediment may influence macrophyte productivity. Other edaphic factors that influence macrophyte productivity include soil drainage, sediment oxidation, exchange of interstitial water, nitrogen nutrition and sulphide concentration (Burdick *et al.* 1989). Edaphic factors controlled the height of *Spartina alterniflora* plants, with longer plants growing at the waters edge (stream side). Sediment characteristics also influence submerged macrophyte colonization and growth. Biomass has been found to vary with sediment texture but this has often not been linearly related to sediment grain size. It has been suggested that texture plays the role of surrogate variable for a complex group of variables related to fetch, slope and current velocity. Grain size also affects nutrient movement and retention within the sediment (Anderson and Kalff 1986a, 1986b and 1988). However, Hanekom and Baird (1988) found that the spatial variation in the distribution and biomass of *Zostera capensis*, in the Kromme estuary, southern African, was not significantly related to sediment particle size.

The sediment stability of a system influences emergent and, particularly, submerged macrophyte colonization. For example, Congdon and McComb (1981) reported that peak standing crop of *Ruppia* occurred when river flow was low. *Ruppia* was more productive in sheltered lagoons and bays where water currents and wave action were low and sediments finely grained. In systems where the sediment is constantly being modified by dynamic processes, submerged macrophytes are absent. This is the case in the Palmiet River estuary where strong water currents and frequent flooding result in the removal of established rooted plants (Branch and Day 1984). On concluding his survey of the small estuaries of Natal, Begg's (1984b) general impression was that submerged macrophytes occur only in systems where the semi-permanently closed mouth results in stable water levels and sediment for approximately one year.

The reduction of freshwater inflow into the Kromme estuary, over the past decade (due to the construction of two dams) has led to increased sediment stability. This has resulted in an increase in *Zostera capensis* biomass and areal distribution (Adams and Talbot 1992). Prior to this, Hanekom and Baird (1984 and 1988) found that fluctuations in the biomass of *Zostera capensis* in the Kromme (South Africa) were related to flood events. Despite the drop in salinity at the time of flooding, these authors concluded that silt deposition, rather than the lowered salinity, was the main cause of the total loss of beds in the coves and sheltered areas. In the more turbulent reaches plants were abraded but not completely removed. Other studies in South African estuaries have shown that changes in *Z. capensis* biomass are linked to flooding activities rather than seasonal influences (Edgecumbe 1980, Talbot *et al*. 1990b). Freshwater impoundment dampens the frequency of floods and sedimentary disturbances. This results in an increase in submerged macrophyte biomass.

Mouth dynamics

Many southern African and Australian estuaries, are seasonally closed at the mouth (Fromme 1985, Van Heerden 1985, Lukatelich *et al*. 1987). Impoundment of freshwater reduces the frequency of floods that flush out accumulated sediment in the mouth. Freshwater deprivation thus causes an increase in the frequency of mouth closure. Opening and closing of the mouth results not only in changes in nutrient exchange and salinity (the effects of which have been reviewed above), but also in fluctuations in water depth over a time scale which may severely impact macrophyte communities.

In the Bot river estuary (southern Africa) that had been closed to the sea for four years, Bally *et al*. (1985) found that contributions to the total primary production of the system were of the order: 72% by submerged macrophytes, 14% emergent reeds, 7% benthic diatoms, 7% phytoplankton. The submerged macrophytes were thus clearly the major primary producers in this system. Following the opening of the mouth, it was conservatively estimated that over 80% of the submerged macrophytes were left stranded. Emergent macrophyte beds that had become established near the mouth, were also washed out to sea.

In the Wilderness lagoon (southern African), Weisser and Howard-Williams (1982) found that encroachment by emergent macrophytes was associated with dropping water levels during periods of low freshwater input when the system was closed to the sea. On the other hand, Howard-Williams and Liptrot (1980) found that primary production in a southern African estuary, was unchanged when the mouth closed for a four month period. The major primary producers in the system were: *Zostera capensis*, *Ruppia spiralis* and the phytoplankton. After the mouth had been closed for a year, the dense *Enteromorpha* mat disappeared. However, the authors speculate that this was due to an increase in grazing by birds, particularly coot, or to the reduction in salinity, rather than to a change in water depth.

Onrus lagoon (southern Africa) was a deep estuary until the 1940's. When the water upstream was dammed, the annual floods could no longer sweep the estuary clear of silt deposition. The mouth consequently closed, salinity decreased and the silt was colonized by dense growths of *Phragmites* (Branch and Branch 1985). In many Natal estuaries, the intertidal zone has been lost due to sedimentation caused by soil erosion in the catchment and due to tidal restriction. This has led to *Phragmites* encroachment and loss of habitat diversity.

Adequate freshwater input ensures that the mouth of the estuary remains open, allowing tidal exchange. Tidal exchange is important as salt marsh plants are alternately drained and inundated by tidal action. Salt marsh plants occur in distinct zones along an elevation and tidal inundation gradient. If the tidal range is restricted, for example by mouth closure, then the zonation and diversity of plants is lost. In periodically closed South African estuaries, mouth closure can result in increased water levels. Prolonged inundation can affect marsh plants. Factors affected by flooding include: inhibition of leaf growth, inhibition of stem extension, inhibition of photosynthesis, promotion of extension growth, senescence and reduced plant productivity (Jackson and Drew 1984).

Studies have shown that submergence of marsh plants eg. *Spartina alterniflora* may lead to root oxygen deficiencies, elevated soil sulfide concentrations and decreased plant N uptake that eventually reduces plant productivity (Wilsey *et al*. 1992). Gradients in primary productivity of marshes relate directly to soil waterlogging with increased distance from tidal creeks (Linthurst and Seneca 1980, Howes *et al*. 1981, Mendelssohn and McKee

1988). Each species has a distinct range of tolerance to depth of water and duration of tidal flooding. The impact that changes in water level will have on plants will depend on the duration, intensity and frequency of the event as well on the phenology of the plant at the time (Ernst 1990). Inundation during the growing season are generally harmful to most species (Olff *et al*. 1988).

Reduction in freshwater flows also results in marine sediments moving upstream due to tidal flow. Since the construction of the Churchill and Charlie Malan dams on the Kromme river, the migration of lobes of marine sand upstream have increased (Reddering and Esterhuysen 1983). Dams built above the Bushman's River estuary have led to marine sand penetrating 4 km upstream covering eelgrass and mud prawn beds in the process (Branch and Branch 1985). In severe cases habitat alteration occurs as sand bed communities replace mud bed communities.

Light related effects

The underwater irradiance environment, determined by water turbidity and depth, is perhaps the most important factor determining the distribution of submerged macrophytes. According to Chambers and Kalff (1985) light limits the maximum depth of colonization as well as influencing the depth of maximum biomass. While Congdon and McComb (1979) found that experimental shading of *in situ Ruppia* populations, in a shallow (< 1m deep), Australian estuarine basin, severely reduced productivity. An 80% reduction in irradiance completely precluded *Ruppia* after 100 days.

Howard-Williams and Allanson (1978 and 1979) examined the depth distribution and temporal changes in submerged macrophyte and macroalgal biomass in a brackish, coastal lake. They concluded that distribution was controlled by irradiance. The lower depth limit of the macrophytes was at 5-10 % of surface irradiance. Historical data showed that the macrophyte beds encroached into deeper water during dry periods, when water clarity improved, and regressed during rainy periods, when inputs of humic laden freshwater increased.

In southern African, Natal estuaries, which are notably turbid, Begg (1984a and b) reported that submerged macrophytes were never dominant, although they did occur in the closed, clear estuaries. *Zostera capensis* was only found in one estuary. *Potamogeton pectinatus* was more common but, in terms of energy input, the filamentous alga *Chaetomorpha*, which bloomed in winter when water transparency was high, played the more important role. However, under these turbid conditons the photosynthetic production by submerged macrophytes is negligible and the major production of organic matter is by emergent marsh plants (Branch and Branch 1985).

Water motion related effects

Water motion is the underlying factor controlling many other physical factors of importance to estuarine macrophytes. Such factors include water clarity, sediment dynamics and mouth dynamics. These aspects have been reviewed above. Water motion also affects macrophytes directly and was, therefore, considered separately.

In the Wilderness lake system (southern Africa), Weisser and Howard-Williams (1982) found that, temporal and spatial decreases in submerged macrophyte biomass were related to increases in wave action and turbidity. Congdon and McComb (1979) found that the productivity of *Ruppia* spp. in Australian estuaries was highest in sheltered lagoons and bays where water currents and wave action were low. Furthermore, Branch and Day (1984) found virtually no attached macrophytes in the Palmiet estuary (southern African) due to the high water velocity. During winter, when maximum water velocity exceeded 1.14 m s^{-1}, *Enteromorpha* was the only macrophyte present and that was on rocky substrata near the mouth. During summer, when flow was slower (maximum speed of 0.96 m s^{-1}), a *Cladophora sp.* was present over most of the estuary.

Howard-Williams and Liptrot (1980) reported that submerged macrophytes were absent from the main channel of the Swartvlei estuary (southern Africa) because of the current speeds of 1.2 - 1.4 m s^{-1} that had been measured over spring tides.

Summary

Of the estuarine flora, the emergent macrophytes are the most productive and under natural conditions there does not appear to be a significant difference between intertidal salt marsh and freshwater wetlands. However, the highest reported productivities are for freshwater swamps, dominated by *Phragmites*, which receive high nutient loads derived from human activities.

There is no evidence to suggest that, within the range 0-40 ppt, salinity significantly affects productivity, although clearly it controls species composition. Even rapid changes in salinity of up to 15 ppt, provided they are stable, lead to the replacement of species. However, none of the emergent macrophytes can tolerate protracted periods of hypersalinity (> 40 ppt) and such conditions lead to a loss of primary and secondary productivity.

Emergent macrophyte communities act as traps for suspended particulates and associated nutrients and may therefore act as nutrient sinks during the growing period. However, there may be considerable export of nutrients from marshes during periods of seasonal die back and when water flow is rapid. In fact, despite their ability to reduce water speeds, the emergent macrophyte communities are destroyed by high water velocities. However, because of their capacity for vegetation reproduction, the plants can rapidly colonize new substrata made available by gradually changing water levels. These communities are not significantly affected by water turbidities.

Although more productive than the phytoplankton, the submerged macrophytes and macroalgae are generally less productive than the emergent macrophytes. As with the emergent species, productivity is little affected by salinity in the range 0-40 ppt, but hypersaline conditions lead to considerably lowered species diversity and diminished productivity. Inputs of nutrients lead to increased productivity but the response may be complicated by concommitant changes in turbidity associated with increased phytoplankton productivity. Turbidity and water motion are the major factors controlling the distribution of these communities. Phytoplankton blooms, high levels of dissolved humics, wave action and high water speeds all lead to diminished production. As well as being less resistant to water motion than the emergent species, the submerged macrophytes are less able to reduce water velocities and consequently less able to trap particulates and dissolved nutrients.

FLoating macrophytes are usually only a minor component of estuarine and brackish water bodies.

3. PHYTOPLANKTON

Introduction

By definition phytoplankton are those microalgae which are suspended in the water column. Thus, although some species have limited motility, their spatial distribution, in the horizontal and vertical dimensions, is controlled primarily by water motion (either as mass flow or turbulence) which is strongly influenced by freshwater input. Another major factor controlling the distribution of phytoplankton is growth rate which is affected by freshwater inputs via its effect on numerous other abiotic factors.

The effect of adding freshwater is not simply to reduce salinity. Freshwater inflow may also bring in new dissolved nutrients and thus directly affect the water column nutrient levels, or it may induce turbulence which mixes benthic regenerated nutrients into the euphotic zone. Thus freshwater inputs indirectly controls the availability of nutrients to phytoplankton. Freshwater inflow also affects water turbidity either by bringing in suspended particulates or dissolved humics, or by creating/reducing turbulence and thus altering the extent to which particulates are maintained in suspension. The turbulence, or mixing depth, also determines the duration for which phytoplankton cells are exposed to high near-surface irradiances or mixed below the euphotic zone. Turbulence may be induced by rapid flow on the one hand, or reduced by salinity induced stratification.

Turbidity is thought to be a major factor controlling phytoplankton production and chlorophyll-a distribution in estuaries. However these conclusions are based on data from large overseas estuaries where horizontal and vertical dimensions are usually an order of magnitude larger than those of South African estuaries (Hilmer and Bate 1991). Our estuaries are shallow and therefore, high turbidity due to sediments brought in by freshwater flow does not necessarily mean light limitation for phytoplankton. Indeed in the St. Lucia estuary (southern Africa) Fielding *et al*. (1991) found that under conditions of extreme turbidity, chlorophyll-*a* was present in the water. The average depth of St. Lucia is 0.96 m and the water column is well mixed by wind-driven wave action.

As Drinkwater (1986) writes: "Freshwater induces important circulation patterns, effects vertical stability, modifies mixing and exchange processes, and influences nutrients and primary production." Further, he writes: "Light reduction from heavy silt loading, prevention of nutrient addition to the surface layer by strong vertical stability, or rapid advection such that the flushing time exceeds the time scale of phytoplankton growth will act to reduce production. On the other hand, in river plumes where freshwater and saltwater are actively mixed, primary production is usually high."; and: "In regions where there are sufficient surface nutrients vertical stability imposed by runoff helps to maintain phytoplankton in the euphotic zone thereby enhancing production."

Clearly the effect of freshwater on the species composition and production of phytoplankton is via a complex interaction of abiotic factors. Smetacek (1986), in reviewing the literature on the impact of freshwater on phytoplankton production, writes: "Freshwater discharge has a twofold effect: a) it introduces allochthonous dissolved and particulate materials and b) it drastically modifies the structure and dynamics of the physical environment. Because of the wide range of variability associated with freshwater discharge (depending on its magnitude and seasonality, the drainage basin and the hydrography/topography of the receiving environment) its impact on the biological processes varies accordingly. Further, such environments are inherently heterogeneous, both spatially and temporally because of the environmental gradient maintained by the admixture of fresh and marine waters.".

The structure of this section of the review is therefore rather loose. Where possible studies have been separated into those focussing on nutrient effects and those focussing on flow rate related effects. Both types of study usually include salinity changes and these effects are discussed simultaneously. Seasonal (temperature and irradiance) effects are also discussed together with whichever other factor is being considered. A brief review of general productivity levels is also given to provide some background.

Comparative Productivities

On the whole, estuaries are rich and productive systems (Odum 1970) and *in situ* production usually exceeds the rates of import of organic material (Correll 1978). Attached macrophytes are usually the dominant primary producers, having much higher rates per unit area. Published estuarine phytoplankton rates generally fall between 13 and 346 g C m^{-2} y^{-1}, while macrophyte productivities typically range from 200 to 3000 g C m^{-2} y^{-1} (Kennish 1986). However, due to the variability in the morphology, meteorology, chemistry and biology of estuaries, the relative contributions by macrophytes and phytoplankton to total system production is variable.

For example, Lee and Olsen (1985) found that phytoplankton contributed only 10% to total system production in a USA, coastal lagoon. In contrast, in a shallow cove off Chesapeake Bay, Mountford (1980) found that phytoplankton contributed 70% (they occupied 87% of the area of the system), while in a nearby cove, Nixon and Oviatt (1973) found that phytoplankton contributed only 20%. In Swartvlei, a southern African brackish coastal lake, Howard-Williams and Allanson (1978 and 1979) found that, despite covering 72% of the area, phytoplankton only contributed 6% to total production. Similarly, in a nearby, mesotrophic estuary which had been closed to the sea for 4 years, Bally *et al.* (1985) found that phytoplankton contributed 7%.

As mentioned above, rates of production are extremely variable. So also are the units that are used and the relationships between biomass, cell numbers and chlorophyll levels. Some idea of typical relationships are given in Mountford's (1980) study in a mesotrophic, shallow, muddy cove, off Chesapeake Bay. He found total cell counts averaged 50 cells μl^{-1}, with a maximum value of 438 cells μl^{-1}. Chlorophyll-a concentrations averaged 16 $\mu g\ l^{-1}$, with a maximum of 32 $\mu g\ l^{-1}$. Cell numbers did not correlate with chlorophyll concentrations, indicating a decrease in chlorophyll per cell from 0.57 ng $cell^{-1}$ to 0.28 ng $cell^{-1}$ during bloom periods. Productivity per unit chlorophyll was highest in spring, when net photosynthetic rates reached 110 g $O_2\ mg^{-1}$ chl-a h^{-1}, but per unit volume, productivity was highest in summer (20 mg O_2 mg 1 chl-a h^{-1} and 400 mg $O_2\ m^{-3}\ h^{-1}$). Annual phytoplankton productivity was estimated at 97.6 g C $m^{-2}\ y^{-1}$ (Table 4), which is close to the average of 100 g C $m^{-2}\ y^{-1}$ for coastal ocean waters.

Nutrient related effects

Flint (1985) examined the effect of riverborne nutrient inputs in a shallow (<5 m), muddy estuary (Corpus Christie Bay, Texas) which is characterized by low annual rainfall (700 mm y^{-1}), low freshwater input with low nutrient loadings, high evaporation rates, small tidal flushing and salinities averaging 30 ppt (range:10-38 ppt). After 11 years of monitoring, Flint (1985) found a strong positive correlation between rainfall in the catchment and phytoplankton primary production. However, despite this he found that at least 90% of the phytoplankton production was supported by nitrogen recycled from sediments. Nutrients brought in by the freshwater pulses boosted production in the short term and recharged the nutrient pools, thus sustaining productivity in the long term. In reviewing the literature Flint found that some authors found that freshwater inputs had positive effects but others found that freshwater pulses severely impacted the resident communities and had a negative effect on production.

Malone *et al.* (1988), studied the mesohaline reaches of Chesapeake Bay (8-14 ppt) and found that maximum chlorophyll-a concentrations occurred in spring when salinity was low and nitrate inputs were high due to peaks in riverine inflow. In contrast to biomass (chlorophyll-a), productivity peaked in mid- to late summer. The authors concluded that riverine nitrate input controlled phytoplankton biomass but irradiance and temperature controlled productivity. However, the level of summer productivity was sustained by recycling the nitrogen that was delivered the previous spring. In South African estuaries rainfall is erratic and thus, definite seasonal patterns of phytoplankton production, i.e., regular spring blooms, are absent. Responses in our estuaries are more opportunistic and related to episodic freshwater discharges (Hilmer 1990, Allanson and Read 1987).

A frequent consequence of reduced freshwater in South African estuaries is closure of the mouth. Consequent changes in salinity, turbidity and nutrients levels may affect the phytoplankton community. Furthermore, under these circumstances the estuary becomes particularly sensitive to pollution and eutrophication, irrespective of whether the salinity increases or decreases. Both these processes will affect phytoplankton species composition and productivity.

The effect of the Grevelingen estuary being cut off from the sea was monitored by Vegter (1977). He found that there was an increase in phosphate being released from decomposition of benthic detritus. Nitrate concentrations decreased to less than 2 μM but ammonium concentrations were generally unchanged although variable (10-30 μM). Salinity stayed constant at about 35 ppt. Average and maximum daily phytoplankton production values also showed little change (Table 4). Integrated annual production was 146 g C m^{-2} and 200 g C m^{-2} in the two years prior to closure, and 175 g C m^{-2} after closure.

Drinkwater (1986) presents a summary of the role of freshwater on coastal marine ecosystems. The systems which he reviews are ones where riverine flow is sufficient for the freshwater plume to occur in the nearshore. In smaller systems, with less flow, this mixing zone may occur within the estuary. The processes and the way in which they are affected will be similar in either case. The only major difference will be in total water depth. His conclusions are therefore directly applicable to estuaries.

Drinkwater found that phytoplankton blooms in the Bay of Brest, are generated by the pulses of nutrients discharged by the rivers even though high tidal mixing and rapid exchange between the Bay and adjacent shelf waters prevent eutrophication. In contrast, in the southern North Sea, eutrophic conditions have even observed during the growing season. Off the German coasts these conditions can be destroyed by intense mixing under storm conditions. The most obvious effect of eutrophication is an increase in the frequency and strength of phytoplankton blooms but a further effect is its influence on species composition. Along the Dutch coast eutrophication is believed to have resulted in a shift from a diatom to a flagellate dominated population.

In less saline, shallow systems with high nutrient loads, the pattern is typically one of increased phytoplankton blooming, often of nuisance or toxic species. Subsequent decomposition of the bloom leads to a high biological oxygen demand (BOD) and the death of much of the fauna (zooplankton and fish). However, Balls *et al.* (1989) found that nutrient additions to a shallow, freshwater lake (England) did not lead to consistent increases in chlorophyll-*a* levels. Instead, chlorophyll-*a* correlated with zooplanktiverous fish and was inversely correlated with zooplankton numbers. The authors conclude that zooplankton grazing is the major determinant of phytoplankton biomass.

The effect of nutrient loading, on species composition in a tidal freshwater system, is described by Moss and Balls (1989). They found that the upstream community was dominated by pennate and centric diatoms while the eutrophic zones downstream were dominated by Cyanophyta. Moss *et al.* (1989) found a correlation between total phosphorus and growing season chlorophyll in this same system, impling that phosphorus was limiting. This explains the dominance of the nitrogen fixing Cyanophyta in the eutrophicated zones. However, Moss *et al.* (1989) point out that the generation to wash out time ratio is critical for population development. Although the former may be controlled by nutrient availability, the latter will be determined by water velocities. They also re-emphasize that zooplankton grazing may be important in determining phytoplankton biomass and may also affect species composition, large phytoplankon species being relatively immune to grazing by zooplankton and therefore likely to predominate in the presence of heavy grazing.

The phytoplankton species composition of a mesotrophic, shallow (<3.5 m), brackish (5-15 ppt), muddy cove (Osborn Cove) off Chesapeake Bay is described by Mountford (1980). The maximum ebb-tide velocity measured in this system was 42 cm s^{-1} and the average turnover time was about 9 days. The phytoplankton were dominated by microflagellates with periodic blooms of other forms. In midsummer there was a bloom of the flagellate *Anisomonas longifilis* and the dinoflagellates, *Prorocentrum minimum*, *Katodinium rotundata* and *Gymnodinium nelsoni* bloomed annually. Diatom abundance followed a typically "riverine" pattern with a spring bloom and a secondary maximum in late summer. Important species were *Thalassiosira sp.* (or *Cyclotella sp.*) and *Cylindrotheca closterium*.

The phytoplankton communities of the St. Johns River (a Canadian freshwater system) has been described by Yount and Belanger (1988). Small unicellular Chlorophyta (especially *Chlorella* and *Chlorococcum*) were numerically dominant. Areas receiving high nutrient loads had high chlorophyll concentrations (up to 187 mg m^{-3}) and high counts of blue-greens (Cyanophyta) such as *Anabaena circinalis*, *Anacystis* and *Lyngbya*. Blooms of the former two species have historically been associated with fish kills. In less nourished river sections chlorophyll-*a* concentrations were typically low (1-6 mg m^{-3}; Table 4) but there was a diverse diatom population (*Cocconeis*, *Synedra*, *Fragilaria*, *Amphora*, *Navicula*) and common Chlorophyta included *Scenedesmus*, *Ankistrodesmus* and *Pediastrum*. A bloom of the filter clogging *Chrysophyte*, *Dinobryon*, (9 filaments ml^{-1}; 10 mg chl m^{-3}) and a bloom of *Anabaena circinalis* (1365 filaments ml^{-1}; 45.6 mg chl m^{-3}) were also noted.

Water motion related effects

Estuarine circulation is important as it controls water residence and phytoplankton turnover time (Callaway and Sprecht 1982 in Peterson and Festa 1984). In some estuaries rates of physical removal may dominate over rates of *in situ* production. For example, if water residence time is small (in the order of hours or days), development of phytoplankton concentrations by *in situ* processes may be restricted because maximum or full blooms may take longer (days or weeks) to develop.

The diversion of freshwater for hydroelectric development resulted in a reduction in the freshwater supply and flow through the Eastmain River Estuary (Canada). Ingram *et al.* (1985) examined the consequences. Salinity increased from 0 ppt up to 8 ppt over the first three months and tidal amplitude increased. Chlorophyll-*a* levels which had ranged from 1 to 1.5 mg m^{-3}, rose to 5 to 10 mg m^{-3} at the mouth of the estuary while offshore values remained between 0.5 and 2.5 mg m^{-3} (Table 4). The increase in chlorophyll within the estuary is ascribed to the reduction in net outward water velocities, which dropped to zero.

Table 4 Published phytoplankton biomass (chlorophyll-a concentration) and productivity values for estuaries and comparable systems (high fw = high, and low fw = low freshwater discharge/flow).

Biomass (μg chl-*a* l^{-1})	Production (g C m^{-2} y^{-1})	Conditions	Reference
1.0 - 1.5	-	0 ppt, high fw	(1)
5.0 - 10	-	8 ppt, low fw	(1)
0.5 - 2.5	-	35 ppt, offshore	(1)
1 - 6	-	< 1 ppt, oligotrophic	(2)
< 187	-	< 1 ppt, eutrophic	(2)
16	97.6	5-15 ppt, < 3.5 m depth	(3)
< 1.6	-	23-31 ppt, high fw, spring	(4)
0.5 - 8.0	-	25-31 ppt, low fw, summer	(4)
-	146-200	35 ppt, mouth closed	(5)
2.7 - 5.1	-	0-35 ppt, oligotrophic, high fw	(6)
0.4 - 6.0	-	8-16 ppt, low fw	(7)

References:

1. Ingram *et al.* (1985)
2. Yount and Belanger (1988)
3. Mountford (1980)
4. Therriault and Levasseur (1986)
5. Vegter (1977)
6. Branch and Day (1984)
7. Bally *et al.* (1985)

There were also changes in species composition (Ingram *et al.* 1985). Prior to the diversion small microflagellates consistently accounted for over 60% of the enumerated cells while larger cells made up the bulk of the biomass (both in the estuary and offshore). Subsequent to the diversion, *Skeletonema costatum* and a *Gymnodium sp.* which were important in the offshore became important in the estuary, while the bloom consisted of a diatom species which had not been encountered offshore, *Cylindrotheca fusiformis*. The change in species composition is ascribed to the increased marine influence, while the bloom is ascribed to the reduced flushing out of cells and to the increase in nutrients in the water column. All these being the result of the reduced water velocity. It was noted that nutrient concentrations were not correlated with salinity.

Smetacek (1986) reports a similar situation in Northern San Francisco Bay which has several rivers flowing into it. It supports large diatom (predominant l0 x *Thalassiosira sp.* and *Skeletonema costatum*) blooms during summer when discharge is moderate but a low biomass (mainly of flagellates) during winter when discharge is high. The conclusion is that high flushing rates prevent the normal bloom diatoms from maintaining themselves in the estuary while moderate flows allow the build up of high biomasses. During a drought year no blooms were observed. This may have been due to the change in the physical structure or an increase in benthic grazing. The abundance of juvenile striped bass which feed on mysids (which feed on the diatoms) was also severely reduced during that year. Variations in freshwater flow can thus have far reaching effects.

In contrast, southern San Francisco Bay which receives little freshwater directly and is shallow and well-mixed, has a low phytoplankton biomass (mainly nanoflagellates) despite high nutrient levels (Smetacek 1986). However, when low salinity water does enter, stratification develops and large diatom blooms accumulate in the surface water. It appears that benthic grazing, which normally controls the phytoplankton, is no longer effective when the water column is stratified. Thus, stratification as a result of freshwater input, enhances phytoplankton production.

On the other hand, in Chesapeake Bay, despite the high biomass of zooplankton and benthic grazers, there are substantial diatom (mainly *Skeletonema costatum*) and dinoflagellate (mainly *Prorocentrum marie-lebouriae*) populations in the shallow well mixed areas with high water retention times (Smetacek 1986). In the Potomac Estuary, the dinoflagellate, *Katodinium rotundatum* bloomed in a winter when freshwater discharge was high, while the diatom, *Chaetoceros sp.* bloomed in a winter with low discharge (Smetacek 1986).

In the Belt Sea (Kiel Bight) which has a fresh water surface layer of 10-15 m deep there is usually a spring bloom of diatoms when salinity is low, and an autumn bloom of *Ceratium* spp. (dinoflagellate) when the freshwater flow decreases and stratification is weaker. Nanoflagellates are of importance only in late spring and are heavily grazed by the high biomass of zooplankton (including copepods), which attain a maximum biomass during late spring and summer. The summer phytoplankton are dominated by medium and large diatoms and dinoflagellates. A similar pattern is observed in St. Georges Bay in Canada where there is salinity stratification and the water has a fairly long residence time. In the Norwegian fjords a spring diatom bloom occurs before the peak in seasonal runoff but a second bloom, of a different diatom species may develop in the low salinity surface layer during peak runoff in early summer. Smetacek (1986) concludes that: "Environments subject to freshwater discharge, in spite of continuous or periodic flushing, nevertheless maintain resident populations of characteristic phytoplankton and zooplankton species."

In the lower St. Lawrence Estuary, Canada (Therriault and Levasseur 1986), the spring peak in freshwater influx delays the spring diatom bloom by decreasing eddy exchange between the surface (salinity 23.5 ppt) and deeper (salinity 29-31 ppt) layers, thus preventing seeding. The autumn bloom also terminates at the same time as the freshwater influx increases. However, the increase in wind velocity at this period and the absence of a correlation between salinity and freshwater input, indicate that this termination is due to light limitation as a result of a deepening of the mixed layer.

Therriault and Levasseur (1986) also found that, during the spring and autumn periods, when freshwater discharge is high, there is a positive spatial correlation between salinity (23-31 ppt) and chlorophyll-a concentration. At such times chlorophyll (mainly microflagellates) concentrations are low, ranging from <0.1 to 1.6 mg m^{-3}. The correlation is not because of a direct salinity effect, but rather because the flushing rate is such that phytoplankton biomass can only accumulate in downstream (i.e. more saline) areas. In contrast, in summer (when the freshwater inflow is low and the average salinity is slightly higher (25-31 ppt)) there is no spatial correlation between salinity and chlorophyll (0.5-8 mg m^{-3}). During this period high concentrations of phytoplankton are associated with regions of upwelling and regions of less turbid water. Thus one river plume which contains clear, fresh water (0 ppt) has high chlorophyll concentrations even though the discharge is small, while another which is turbid and introduces a larger volume of saline (26 ppt) water, has lower chlorophyll concentrations.

Peterson and Festa (1984) present a numerical model of phytoplankton production in San Francisco Bay. The model incorporates the effects of river flow and irradiance as a function of suspended solids and phytoplankton (self shading). They divide the system into 3 zones from a water circulation point of view: the river section where flow is seaward; a transition zone where surface water flow is seaward and bottom flow is zero; and an upper estuarine zone where the surface flow is seaward but the bottom flow may be landward. Phytoplankton in the surface water will therefore be lost to the system while those in the bottom water may be retained.

The model highlights the importance of the balance between phytoplankton sinking rates and water circulation in the development of high biomass and blooms. "A basic role of estuarine circulation in controlling phytoplankton development can be illustrated by examining the relation between water residence and phytoplankton turnover time (Callaway and Sprecht 1982, in Peterson and Festa 1984). A measure of *in situ* phytoplankton turnover time is defined here as the ratio of the standing stock to its integral photosynthetic production. In some estuaries or portions thereof, and at certain times of the year, rates of physical removal may dominate over rates of *in situ* production.

For example, if water residence time is small (on the order of hours or days), development of phytoplankton concentrations by *in situ* processes may be time limited because maximum or full blooms may take longer (days or weeks)." "Field studies demonstrate that bloom development is prevented or destroyed . . when rates of dilution exceed net growth rates (Lack 1971, Lasker 1975, Pingree *et al.* 1976, all in Peterson and Festa 1984). Thus the typical response of phytoplankton biomass to increasing river flow is a reduction in their concentration by the increasing dilution rate (Di Toro 1971, Lack 1971, both in Peterson and Festa 1984). Bloom development is suppressed in several rivers in England when river flows exceed 10-30 cm s^{-1} (Lack *et al.* 1978, in Peterson and Festa 1984)." "In some instances, during such high river flows estuarine phytoplankton (chlorophyll) concentrations may even appear to be nearly linear when plotted against salinity (Peterson 1979, in Peterson and Festa 1984). A similar response is seen in numerical simulation experiments." Water residence times are also important in terms of nutrient utilization. If retention times are short (days), then there is insufficient time for the phytoplankton to trap the nutrients and the latter will be washed out to sea.

Water circulation also plays a significant role in phytoplankton dynamics by affecting the depth of light penetration which depends on the concentration of suspended particulate matter, both living and non-living (Peterson and Festa 1984). Generally the concentrations of suspended particles in estuarine water are high and light is rapidly attenuated. Peterson and Festa (1984) found that concentrations of suspended sediments of 10-100 mg l^{-1} strongly suppressed phytoplankton biomass and these values are typical for estuaries (Milliman and Meade 1983, in Peterson and Festa 1984). Living phytoplankton also attenuate the light. If chlorophyll concentrations reach 200 μg l^{-1} (eg. in the Potomac River: Peterson 1980) self-shading becomes an important factor in controlling phytoplankton productivity and biomass. Below 100 mg chl m^{-2}, shelf shading is not important and at less than 2 μg l^{-1}, water absorbs more light than does the chlorophyll.

Stross and Sokol (1989) examined the spatial and temporal variations in the attenuation of irradiance in the Hudson River Estuary. In the zone where salinities ranged from 0.1 ppt to 21 ppt, photic depth ranged from 0.6 m in late winter, when freshwater inflow was maximal, to 4.3 m in summer. By contrast, photic depths in the more saline reaches, ranged from 3 to 6 m (Malone 1977). In this study the increase in photic depth is simultaneous with the increase in phytoplankton. The spatio-temporal distribution of chlorophyll ranged widely from 2 to 50 mg m^{-3} at different times and places. Overall the phytoplankton were responsible for 20% of the attenuation of the photosynthetically active radiation (PAR), with contributions varying from 2.5% in the fresher regions (0.1-0.2 ppt) to 61% in the mid regions (1-4 ppt).

Summary

Biomass (chlorophyll-a) and productivities quoted in the literature reviewed above, are summarized in Table 4. On the whole, phytoplankton productivity per unit area is an order of magnitude less than that of macrophytes. However, the area of an estuary or brackish lake which is occupied by phytoplankton is often so large that phytoplankton contribute more to total system primary production than do macrophytes. Furthermore, unlike macrophytes, phytoplankton may contribute substantially to grazing food chains.

Up to 40 ppt, salinity does not affect phytoplankton productivity, it only affects species composition. The fact that low production is often associated with euhaline conditions, is a nutrient effect: lower nutrient availability usually being associated with a stronger marine influence. Indeed nutrient availability appears to be the major freshwater related factor controlling phytoplankton production - increased nutrient availability leading to increased production, except in cases of extreme eutrophication when the effect becomes negative. Increased nutrient availability in estuarine waters may result from a number of processes:

- increased nutrient loading in the freshwater input;
- increases in the quantity of freshwater input;
- increases in fresh/seawater flow rates such that benthic regenerated nutrients are mixed into the euphotic zone.

Irradiance is also an important factor. Apart from seasonal and diurnal changes, underwater irradiance levels are determined by water turbidity. This is affected by freshwater inputs in the following ways:

- silt and other particulates in the inflowing freshwater increase turbidity;
- fresh/seawater flow rates which induce mixing may result in the resuspension of settled particulates.

Generally low turbidities, and thus deep euphotic zones, lead to high productivities per unit chlorophyll-a (biomass). However, in shallow estuaries the euphotic zone may be limited by the depth of the system. If phytoplankton biomass accumulates, the phytoplankton themselves may also contribute significantly to the water turbidity.

Productivity per unit area is a function not only of productivity per unit biomass but also of biomass accumulation. These factors control productivity per unit biomass and as such also control biomass accumulation. However, the primary determinant of biomass accumulation is water velocity. Although phytoplankton turnover times are short, and despite the ability of some species to maintain horizontal location by vertical migration, the residence time of estuarine water may be such as to prevent biomass accumulation. These residence times will depend on freshwater flow rates *per se* as well as tidal flow and the condition of the mouth.

4. BENTHIC MICROALGAE

Introduction

In shallow aquatic ecosystems, or those with large intertidal regions, benthic microalgae are often important contributors to primary production (Lukatelich and McComb 1986). Fielding *et al.* (1988) found that benthic microalgal production contributed 22% to the total primary production of the Langebaan lagoon, southern Africa. There was a distinct gradient in biomass of benthic diatoms from the mouth of the lagoon to the head. However in the Bot, a closed southern African estuary Bally *et al.* (1985) estimated benthic microalgae to contribute only 7%. Kennish (1986) lists some production values for benthic microalgae. Values generally lie in the same range as for phytoplankton but are lower than for macrophytes.

Different studies have shown that the distribution and diversity of phytoplankton and benthic microflora is related to physical and biological factors such as temperature, salinity, weather and competition with other organisms. Primary production, microalgal biomass or concentration of chlorophyll-a have been measured to demonstrate these phenomena. Admiraal (1977) noted that benthic diatoms are subjected to a melange of environmental variables which influence the spatial distribution of the community (tidal resuspension and settling of sediments, tidal pumping, precipitation and evaporation, oxygen and carbon dioxide, dissolved nutrients, salinity, temperature, pH, alkalinity).

Studies of estuarine primary production have indicated that factors such as light intensity, day length, temperature, water movement and tidal cycle, sediment moisture and stability, animal activity, and nutrient supply can affect production dynamics of sediment-associated algae (Davis and McIntire 1983).

Grant *et al.* (1986) studied the effect of weather and water movement on diatom films and noticed that diatom films were present on the sediment surface after calm weather and absent after storms. In the Dutch Wadden Sea the negative effects of bad weather were also demonstrated. Hard wind with rain and heavy sea ruptured the coherent sediment layer usually stabilized by a film of diatoms. This resulted in the resuspension of benthic diatoms. which explained the occasionally high numbers found in the phytoplankton of the Wadden Sea (Colijn and Dijkema 1981). Diatom cells attach to sand grains with mucus strands and these films are affected by erosion, burial and exposure. de Jonge (1985) explained the dynamics of the species composition of benthic diatoms in terms of adhesion capacity of diatoms and sediment sorting by currents and waves. Benthic microalgae may be important in binding sediments at the lower end of the littoral zone (Kennish 1986).

In the Yaquina estuary, Oregon, distributional patterns of intertidal diatoms were primarily controlled by mean salinity and characteristics of the sediment (Amspoker and McIntire 1978). Canonical correlation ordered 20 prominent diatom taxa along the salinity gradient and identified possible relationships among certain taxa and selected environmental variables, namely visible light energy and temperature (Karentz and C.D.McIntire 1977). Moore and McIntire (1977) gave the general distributional patterns in the estuary which were controlled primarily by salinity and desiccation gradients and by seasonal changes in light energy available to the flora. Mean species diversity was lowest at sites of prolonged desiccation.

Freshwater input and salinity related effects

McIntire and Overton (1971) and Main and McIntire (1974) found a positive correlation between salinity and benthic diatom biomass. Salinity affected the species composition of the benthic diatom flora but had no apparent effect on the rate of primary production (McIntire and Amspoker 1986). Studies in the Yaquina estuary, Oregon showed a transition of diatom species from a marine to a brackish to a freshwater environment with three different assemblage zones (Wasell and Håkansson 1992).

Table 5 indicates the diatom species associated with specific salinity ranges. From this table it is apparent that specific genera are not necessarily associated with a certain salinity range.

Freshwater input also affects the benthic communities through sedimentary disturbances. In the Columbia river estuary the highest rates of microalgal production were associated with the finer sediments. However there was some evidence to indicate that sandy sites could be productive if sediment disturbance was minimal. For example, the rate of primary production at a sandy site on Quinns Island varied from 7 mgC m^{-2} h^{-1} in June, when freshwater discharge was high, to 189 mgC m^{-2} h^{-1} in September, when the substrate was relatively undisturbed by water movements (McIntire and Amspoker 1986).

Plankton assemblages in spring, summer and fall had fewer diatom species and exhibited a more rapid rate of change in species composition than in winter. Winter assemblages were characterized by many pennate diatoms, apparently dislodged from the benthos during periods of high fresh water discharge and silt loads (Karentz and McIntire 1977).

Table 5 Diatom species associated with specific salinity ranges (freshwater 0-5 ppt, brackish water 5-15 ppt and marine water > 15 ppt, + indicates presence, numeral indicates literature cited).

Species	Fresh	Brackish	Marine
Achnanthes brevipes		+[1]	+[1]
Achnanthes cocconeides		+[1]	+[1]
Achnanthes deflexa	+[1,3]		
Achnanthes delicatula	+[5]		
Achnanthes delicatula ssp. hauckiana		+[5]	
Achnanthes groenlandica var.phinneyi		+[3]	
Achnanthes groenlandics f.jaydei			+[3]
Achnanthes javanica f.constricta		+[3]	
Achnanthes kuwaitensis		+[3]	+[5]
Achnanthes lanceolata	+[1,3]		
Achnanthes linkei	+[5]		
Achnanthes minutissima	+[1,3]		
Achnanthes renei	+[5]		
Achnanthes yaquinensis			+[3]
Achnanthes sp.			+[4]
Actinoptychus splendens		+[4]	
Amphipleura rutilans		+[1]	+[1]
Amphiprora paludosa	+[2]	+[2]	
Amphiprora paludosa var.subsalina	+[4]	+[4]	
Amphiprora sp.			+[4]
Amphora sp.	+[4]	+[4]	+[4]
Bacillaria paradoxa			+[4]
Bacillaria paxillifer	+[1]	+[3]	
Biddulphia aurita			+[4]
Biddulphia longicruris		+[2]	
Caloneis sp.		+[4]	
Campylodiscus daemelianus		+[4]	
Campylodiscus sp.		+[4]	
Ceratulina pelagica			+[2]
Chaetoceros debilis		+[2]	+[2]
Chaetoceros radicans			+[2]
Chaetoceros socialis			+[2]
Chaetoceros subtilis	+[2]		

Table 5 continued	**Fresh**	**Brackish**	**Marine**
Chaetoceros sp.			+[4]
Cocconeis scutellum			+[4]
Coscinodiscus lacustris	+[4]		
Coscinodiscus sp.			+[4]
Cyclotella meneghiniana	+[4]		
Cylindropyxis sp.	+[2]	+[2]	+[2]
Diploneis bombus		+[4]	
Ditylum brightwellii			+[4]
Donkinia sp.			+[4]
Eunotia sp.		+[4]	
Fragilaria striatula var. californica			+[3]
Fragilaria sp.	+[4]		
Gomphonema angustatum	+[5]	+[5]	+[5]
Gomphonema parvulum	+[5]	+[5]	+[5]
Grammatophora angulosa			+[4]
Grammatophora marina		+[4]	+[4]
Gyrosigma varipunctatum		+[4]	
Gyrosigma sp.	+[4]	+[4]	+[4]
Hantzschia virgata			+[4]
Licmophora gracilis			
Licmophora sp.			+[4]
Melosira dubia		+[4]	
Melosira moniliformis		+[1, 3]	
Melosira nummuloides		+[3]	
Melosira sulcata		+[2]	
Melosira sp.	+[4]		
Navicula cohnii	+[5]		
Navicula crucigera		+[3]	
Navicula diserta		+[1]	+[1]
Navicula gregaria	+[3]		
Navicula humerosa		+[4]	
Navicula mutica	+[1,3,5]		
Navicula muticopsis	+[5]		
Navicula viridula var. avenacea	+[1,3]		
Navicula n°2		+[1]	+[1]
Nitzschia angularis		+[3]	
Nitzschia closterium	+[4]	+[4]	+[4]
Nitzschia frustulum var. perpusilla	+[1]	+[1]	

Table 5 continued	**Fresh**	**Brackish**	**Marine**
Nitzschia parvula	+[1]		
Nitzschia sigma	+[4]		
Nitzschia spathulata			+[4]
Nitzschia tranvaalensis	+[4]		
Paralia sulcata		+[4]	
Pinnularia sp.	+[4]		
Plagiogramma brockmanni		+[2]	+[2]
Pleurosigma subsalum or *Gyrosigma subsalum*	+[5]	+[5]	
Pleurosigma sp.	+[4,5]		
Rhopalodia sp.	+[4]		
Stauroneis sp.	+[4]		
Surirella ovata	+[2]	+[2]	
Surirella sp.	+[4]	+[4]	+
Synedra fasciculata			+[3]
Synedra fulgens		+[4]	
Synedra ulna	+[4]	+[4]	
Synedra sp.	+[4]	+[4]	
Tabellaria flocculosa	+[4]		
Thalassionema nitzschioides			+[2]
Thalassiosira decipiens		+[2]	+[2]
Thalassiosira fluviatilis		+[2]	
Tropidoneis lepidoptera	+[4]	+[4]	

References:

[1] Moore and McIntire (1977)
[2] Karentz and McIntire (1977)
[3] McIntire (1978)
[4] Masson and Marais (1975)
[5] Wasell and HÅkansson (1992)

There was a distributional continuum of marine and brackish-water diatom taxa that changed location in the Yaquina estuary with seasonal variation in fresh water discharge. The vertical and horizontal gradients of salinity and desiccation were steep enough to manifest three relatively discrete assemblages, one with typical freshwater taxa and two dominated by species of *Melosira* and *Achnanthes*. There was a difference in the flora between stations continuously or periodically exposed to salinity below 5 ppt and those where the salinity remained above this concentration, a discontinuity that shifted location in relation to patterns of freshwater discharge (Moore and McIntire 1977).

Benthic microalgal biomass also appears to be influenced by nutrients brought in by freshwater input. In a shallow southwestern Australian estuary biomass increased with the onset of riverine nutrient input and decreased when phytoplankton blooms occurred in the water column. The sediment chlorophyll was significantly, positively correlated with salinity, ammonium, nitrate and organic phosphorous and nitrogen concentration in the water column (Lukatelich and McComb 1986).

Temperature related effects

Colijn and Dijkema (1981) discovered low chlorophyll-a values in winter followed by a spring bloom, distinct summer depression and new maximum in autumn. The cause of the summer depression was not explained. Sullivan (1975) studied the epipelic diatom flora of 5 different salt marsh habitats and concluded that differences between communities were closely related to differences in temperature and water level.

Admiraal and Peletier (1980) kept cultures of four benthic diatom species (*Navicula salinarum*, *Amphiprora cf. paludosa*, *Navicula arenaria* and *Gyrosigma spencerii)* at the surface of a mudflat in order to measure division rates. The mean temperature was the predominant factor regulating cell division rate. Hot, sunny weather and high air temperatures resulted in the highest cell division rates. These observations apparently contradict indications that some benthic diatoms are inhibited by high summer temperatures (Hopkins 1964).

Water motion related effects

Under calm conditions and low wave heights, the accumulation of diatoms on the sediment surface are readily observed (Schaffer 1988). Benthic diatoms tend to remain in the upper few mm of sediment if the system is undisturbed, but can survive relatively long periods of burial when the sediments are mixed (McIntire and Amspoker 1986). In the Langebaan lagoon (Fielding *et al.* 1988) found that the highest chlorophyll-a concentrations occurred in the top 1 mm of sediment, declining to 35 % of surface concentration 5 cm below the surface. In the same system highest biomasses occurred in the most sheltered areas and reached 18.9 $g.m^{-2}$ in the top 30 cm of sediment. Diatom biomass was highest at subtidal and low-tide sites compared to mid- and high-tide sites. In the Dutch Wadden sea low chlorophyll-a concentrations were found on the exposed sandy stations and maximum concentrations on the more sheltered stations (Colijn and Dijkema 1981).

In the most dynamic zones of a given small estuary, i.e. at the mouth, the formation of ripples takes place. The structure of the ripples is very dynamic in both temporal and spatial scales. The sand particles which accumulate at the crest are avalanched to the lee face and this results in covering of the microalgae. At the same time, microflora associated with the crest are resuspended into the water column (Jenness and Duineveld 1985). Therefore the perturbation of the sediment surface by water movement causes two different but simultaneous processes, resuspension on the one hand and burial on the other. This process depends on the current velocity of the water mass affecting the sediment surface. A current speed of at least 20 cm s^{-1} at 15 cm above the sediment surface is required to initiate ripples having a medium grain size of 245 μm. Above a current speed of 29 cm s^{-1}, complete erosion of sediment layers begin (Jenness and Duineveld 1985).

Sediment related effects

In a Louisiana estuary benthic microfloral production measured at a subtidal site consisting of muddy sand was almost twice that measured at a sandy intertidal site. Productivity at the muddy sand site was influenced by a combination of physical and biological activities (Schaffer 1988). Benthic microalgal biomass, generally measured as chlorophyll-*a* has previously been shown to be related to sediment type, finer sediments having higher chlorophyll-*a* concentration than coarser sediments (Fielding *et al.* 1988).

Davis and McIntire (1983) tested the hypotheses that benthic algal primary production dynamics were controlled by sediment type, tidal height, and season. They reported mean concentrations of chlorophyll-*a* in the top cm of sediment for the entire study period as :

46.2 $mg.m^{-2}$ → SAND
74.7 $mg.m^{-2}$ → FINE SAND
93.7 $mg.m^{-2}$ → SILT.

Properties of the sediments can account for large differences in the structure of diatom assemblages (Moore and McIntire 1977). The limit of the photic zone in sediments is generally from 2 to 5 mm depending on the sediment type and microalgal biomass (Lukatelich and McComb 1986). In the Peel-Harvey estuarine system most chlorophyll was in the top 1 cm of sediment, and less than 10% of chlorophyll-*a* was non-functional. Highest biomass occurred at shallow sites and on coarse sandy sediments (Lukatelich and McComb 1986).

From preliminary microscopic observations of soft sediments in a New England estuary, it appeared that the intertidal epipelic diatom community was vertically organized in the microhabitat according to cell size. Other benthic microalgal communities also have been found to be vertically stratified in, or on, the substrate. Epipsammic diatoms in sandy sediments, periphytic diatoms on hard substrate, blue green algal mats and bacterial-algal associations are examples of such communities (Baillie 1987).

Schaffer (1988) measured the primary productivity and calculated the relative abundance of benthic diatoms species in sandy and muddy sites. The role of sand ($\phi > 55\ \mu m$) as a substratum for benthic diatoms was investigated. On average 13% of the sand grain was occupied by 1 or more diatom cells. The majority of the diatom cells (80 %) in this fraction were present in or on mud coating the sand grain. The preference of benthic diatoms for the mud coating rather than the bare parts of the sand grain stresses the importance of mud ($\phi < 55\ \mu m$) as a substratum for diatoms on the tidal flats. Sand grains act as a physical substratum for colonization by benthic diatoms. Mud particles are aggregates consisting roughly of clay minerals, detritus particles including bacteria, and organic substances that act as an adhesive. Mud is also important as it protects diatom cells against mechanical damage (deJonge 1985). Table 6 documents the occurrence of benthic diatom species in relation to sediment particle size.

Species composition

Benthic microflora can be subdivided into attached and non-attached fractions to sediment particles. The attached or episammic fraction inhabits the sediment surface and consists mainly of diatoms and bacteria with occasional Cyanophytes and Chlorophytes (Harwood 1992), and eventually presents a phytoplankton phase (Talbot *et al.* 1990a). The non-attached or epipelic fraction inhabits deeper layers of the sediment column and has been shown to migrate vertically with tidal rhythm (Palmer and Round 1965, Heckman 1985, Varela 1985). They are primarily motile diatoms, occasionally also filamentous or coccoid Cyanophye, Dinophyte and euglenoid flagellates growing on sand and silt both in the intertidal and subtidal (Harwood 1992). Palmer and Round (1965) postulated that this vertical migration of benthic microflora was a response to the directional stimulus of light.

Table 6 The occurrence of benthic diatom species in relation to sediment particle size. (+ indicates presence, numeral indicates literature cited).

sandy mud	sand	muddy sand	mud	SPECIES
	+[2]		+ +[2]	*Achnanthes curvirostrum*
			+[2]	*Achnanthes delicatula*
	+[1]			*Achnanthes hauckiana*
			+[2]	*Achnanthes punctifera*
	+[2]			*Actinoptychus senarius*
			+[2]	*Amphiprora paludosa*
	+[2]		+ +[2]	*Amphora caroliniana*
	+[1]	+[1]		*Amphora coffeaeformis*
	+[1]			*Amphora exigua*
+[1]	+[1]	+[1]		*Amphora laevissima*
	+[2]		+ +[2]	*Amphora proteus*
	+[2]		+[2]	*Amphora richardiana*
	+[2]			*Amphora sabyii*
	+ +[2]		+[2]	*Amphora turgida*
	+[2]			*Cocconeis disculoides*
	+[2]			*Cyclotella atomus*
	+[2]		+[2]	*Cyclotella caspia*
	+[2]		+[2]	*Cyclotella stylorum*
+[1]		+[1]		*Cymatosira belgica*
	+[2]		+[2]	*Diploneis bombus*
	+[2]		+[2]	*Diploneis littoralis*
	+ +[2]		+[2]	*Eunotogramma laeve*
	+[1]			*Hantzschia virgata var. gracilis*
	+[2]			*Hantzschia virgata var. witti*
+[1]		+[1]		*Navicula cf.cincta*
	+[2]		+[2]	*Navicula abunda*
	+ +[2]		+[2]	*Navicula ammophila*
+[1]	+[1]	+[1]		*Navicula arenaria*
	+[1,2]			*Navicula cancellata*
			+[2]	*Navicula consentanea*
	+[2]		+ +[2]	*Navicula cruciculoides*
+[1]	+[1]			*Navicula crucifera*
+[1]	+[1]	+[1]		*Navicula cryptocephala*

Table 6	continued			
sandy mud	**sand**	**muddy sand**	**mud**	**SPECIES**
+[1]	+[1]	+[1]		*Navicula digitoradiata*
	+[1]	+[1]		*Navicula flatanica*
	+[2]		+[2]	*Navicula forcopata*
	+[2]		++[2]	*Navicula gregaria*
			+[1]	*Navicula hudsonis*
+[1]	+[1]			*Navicula pelliculosa*
	+[1]			*Navicula peregrina*
	+[2]		++[2]	*Navicula salinarum*
+[1]	+[1]	+[1]	+[2]	*Navicula salinicola*
	+[2]		++[2]	*Navicula subapiculata*
	+[2]		++[2]	*Navicula subinflatoides*
			+[2]	*Navicula taraxa*
	+[2]			*Navicula tenera*
	++[2]		+[2]	*Navicula sp#1*
	+[2]			*Navicula sp#2*
	+[2]			*Nitzschia cf. bacillariaeformis*
	+[1]			*Nitzschia dissipata*
	+[1]			*Nitzschia dubiiformis*
	+[2]		++[2]	*Nitzschia fontifuga*
+[1]		+[1]		*Nitzschia laevis*
	+[2]			*Nitzschia panduriformis*
	++[2]		+[2]	*Nitzschia quadrangula*
	+[1]			*Nitzschia spathulata*
	+[1]			*Pinnularia ambigua*
	+[2]			*Plagiogramma tenuissimum*
	+[1]	+[1]		*Pleurosigma aestuarii*
+[1]		+[1]		*Raphoneis minutissima*
	+[2]		++[2]	*Stauroneis salina*
	++[2]		+[2]	*Thalassiosira decipiens*
	+[2]			*Thalassiosira eccentrica*
	+[1]			*Tropidoneis lepidoptera*
	++[2]		+[2]	*Tropidoneis [illegible] istriata*

[1] Colijn and Dijkema (1981)

[2] Schaffer (1988)

The sandy sediment beneath beds of the seagrass *Halodule wrightii* Ascherson in Mississippi Sound support a diverse and productive benthic microalgal assemblage. The sand microflora are important as they represent a readily available food source for consumers resident within the bed. Over an annual cycle (June 89-June 90) virtually all algal cells comprising the sand microflora were small araphid, monoraphid, and biraphid pennate diatoms ($<15\ \mu m$ length). Blue green algae were also present. Two major microfloral groups could be identified:

(1) Epipelic forms which are motile and inhabit the interstitial spaces of the sandy substrate.

(2) Epipsammic forms which are minute in size and live on the flat surfaces and within crevices and fissures of the sand grains. They adhere to sand grains by means of mucilaginous secretions (Daehnick *et al.* 1992).

According to Katoh (1992) the relative abundance of adnate diatoms decreased and that of rosette forming diatoms (eg. *Achnanthes minutissima*) increased with an increase in algal density. The relative abundance of stalked diatoms decreased with an increase in the algal cell density when the algal cell density was greater than 10^5 cells.mm^{-2}. Some of the rosette forming diatoms can attach not only to the substrate but also to diatoms stalks, this means that they have an advantage over other vertically positioned diatoms in competition for space (Roemer *et al.* 1984).

Species can also be classified according to cell size. In Branford Harbour, Conneticut Baillie (1987) found two major types of community organization. Cells were either very small or very large, intermediate-size cells were less numerous. Diatoms were vertically distributed in the sediment along a cell size gradient. Small diatoms dominated the entire photic and oxygenated zones (depth about 1.5 mm). Below 1.5 mm, large diatoms increased in importance and large sigmoid pennates were found almost exclusively in dark anoxic environments (Baillie 1987).

It is reported that adnate species become dominant under strong grazing pressure or physical disturbance. The benthic invertebrates which feed on epilithic algae modify the composition of the algae due to selective grazing of the easily accessible algae, and as a result, adnate species tend to be dominant under strong grazing pressure (Sumner and McIntire 1982, Jacoby 1987, Peterson 1987).

Summary

Benthic microalgae have certain features in common with emergent and submerged macrophytes by virtue of their habitat. Exposure (desiccation), light availability and salinity are factors which effect distribution and biomass. Some studies indicate that within an estuary specific freshwater, brackish and marine benthic microalgal communities can be identified. Being close to the major site of nutrient regeneration, benthic microalgae are likely to be relatively unaffected by nutrient inputs. Some studies have shown that benthic microalgal biomass increases with an increase in riverine nutrient input but eventually is shaded out by phytoplankton blooms. Water currents and sedimentary disturbance are important factors controlling biomass accumulation. Water speeds also determine benthic sediment texture and the accumulation of nutrient rich organics - higher flow rates leading to coarser, nutrient poorer sediments which will support smaller microalgal populations. Benthic microalgal production in mud can be twice that of sand populations.

5. STUDIES ON SOUTH AFRICAN ESTUARIES

Introduction

A considerable amount of work has been done on South African estuaries (in the broadest definition of the word) and several reports summarizing information available prior to the early 1980's have been published. Begg (1978) reviewed the information available on the larger Natal estuaries and subsequently updated this information with field observations and extended the review and his survey to included data on the smaller estuaries (Begg 1984a and b). Basic descriptions of the catchments, morphometry, geology, mouth condition, physico-chemical conditions, hydrology and water transparency are given. Descriptions of the fauna include names of fish and invertebrate species caught, and birds and large vertebrates easily seen during a short visit. The descriptions of the flora of the estuaries are restricted to the more obvious submerged macrophytes, the emergent macrophytes and the fringing vegetation. From his reviews it is apparent that little is known of the phytoplankton and deeper benthic flora. The National Research Institute for Oceanography (NRIO) now EMATEK (Division of Earth, Marine and Atmospheric Science and Technology, CSIR) published a series of reports containing fundamental information on the catchments, flooding frequency, morphometry and mouth condition of individual Cape estuaries. The Council for Scientific and Industrial Research (CSIR) have published a similar series synthesizing the available biotic and related abiotic data for the same Cape estuaries. With the exception of some of Begg's work, these reports are largely descriptive. However, a number of Cape and Natal estuaries have been intensively studied, both at the descriptive level and in terms of processes, over the last decade. Details of these studies are given below.

Natal estuaries

If one excludes the large estuarine lake systems such as St Lucia, most of Natal's systems have surface areas of less than 100 ha. The small size of most of Natal's estuaries have made then vulnerable to human impact and subsequent degradation (Ramm 1990). Begg (1984a and b) points out that the mouths of the Natal estuaries frequently close as a result of the substantial sand transport by littoral drift along the shore. Once the mouth is closed the salinity usually drops and a complete range of estuaries are found: oligohaline (0.5-5ppt) mesohaline (5-18 ppt) and polyhaline (18-30 ppt). Hypersaline estuaries were rare. Although Natal estuaries are notably turbid (Day 1981d), water transparencies were variable. Large open systems are generally more turbid than closed ones and transparencies are reduced in the summer rainy season. The substratum in Natal estuaries is usually muddy sand of fluvial origin.

The reed *Phragmites australis* is common. Trees at the margins range from true mangroves (*Avicennia marina* and *Bruguiera gymnorrhiza*), to lagoon hibiscus (*Hibiscus tiliaceus*), to freshwater mangroves (*Barringtonia racemosa*). Coastal forest may even reach to the waters edge. Grasses include *Echinochloa pyramidalis, Paspalum vaginatum and Stenotraphum secundatum*. Submerged macrophytes are never dominant but do occur in closed clear estuaries. *Zostera capensis* is only found in one estuary. *Potamogeton pectinatus* is more common but in terms of energy input, the filamentous alga *Chaetomorpha,* which blooms in winter when water transparency is high, plays the more important role. Begg deduces from the fauna present, that macrophytes are important in supplying organic detritus which is the basic ingredient upon which energy flow through the estuarine food web depends. The relative importance of phytoplankton production in this regard, in these systems is unknown.

On the basis of his largely visual survey of the condition, flora and fauna of the Natal estuaries, Begg (1984 a and b) concluded that run-off is the single most important physical factor influencing Natal estuarine processes. Although seasonal droughts naturally result in occasional closure, closure of the Natal estuary mouths has become an artificial norm primarily due to siltation which has had a greater detrimental effect than any other single factor. This siltation is largely due to soil erosion in the catchments. Dam construction helps alleviate this problem in that the dams intercept the silt. Dams, however, reduce freshwater inputs and the frequency of scouring floods.

Schleyer and Roberts (1987) point out that bad agricultural practices in the catchments of many Natal estuaries results in heavy siltation and degrades the condition of the estuary. With this increased sedimentation, the reed *Phragmites australis* becomes a problem in the shallower waters, chocking the estuary and reducing the scouring effects of floods. The accumulation and decomposition of detritus in these systems could result in increased oxygen demand and anaerobic conditions within the estuary, impairing the biological functioning of the system (Schleyer and Roberts 1987). These problems have been noted in the Siyaya Lagoon and many other estuaries along the Natal coast. The Natal Town and Regional Planning Commission (NTRPC) are investigating ways of restoring the degraded systems - either by eliminating the *Phragmites* beds or encouraging better farming practices in the catchment.

Phytoplankton productivity has been studied (Allanson and Hart 1975) in the clear (Secchi depth 3-4 m), freshwater Lake Sibaya in northern Natal. Average chlorophyll-*a* concentrations were 2.5 mg m^{-3} (1.5-4.5 mg m^{-3}) over the period 1970-71. The dominant phytoplankter was *Closterium pronum*. The vertical distribution of cells was even except for a maximum at 5 m. Carbon fixation was inhibited at the surface, peaked at about 2 m (6-22 mg C m^{-3} h^{-1}) and declined to <0.5 mg C m^{-3} h^{-1} below 9-10 m. Daily production ranged from 227 mg C m^{-2} day^{-1} under overcast conditions to 1847 mg C m^{-2} day^{-1} (annual average = 807 mg C m^{-2} day^{-1}) cf. 1500-3400 mg C m^{-2} day^{-1} measured by others in tropical and subtropical lakes.

Great Fish, Kariega and Keiskamma estuaries

Allanson and Read (1987) examined the ecology of these three estuaries with particular reference to their differing freshwater inputs over several years. They found that the Great Fish, which has a sustained freshwater input, showed typical estuarine salinity gradients with vertical stratification and brackish middle reaches. Turbidity and nutrient levels (nitrogen and phosphorus) were comparatively high. Chlorophyll-*a* levels were also high, 20.5 $\mu g\ l^{-1}$ on average, with the highest concentrations occurring in the brackish zones. Submerged macrophytes appeared to be absent.

In contrast to the Great Fish, the Kariega is a small estuary with minimal freshwater input. Salinities usually increased towards the mouth but occasionally the head of the estuary became hypersaline (40 ppt) and the gradient was reversed as the mouth remained open at all times. Tidal velocities were sufficient to completely mix the water column and there was no vertical stratification. Nutrient levels were generally very low, being highest at the mouth. It can therefore be assumed that the system depends on internally cycled nutrients. Water turbidity was also low and so were chlorophyll-*a* levels (mean = 4.5 $\mu g\ l^{-1}$).

Thirteen marcophyte species have been found to occur in the marsh areas of the Kariega estuary, namely - *Spartina maritima, Sarcocornia perennis, S. pillansii, Triglochin bulbosum, Chenolea diffusa, Salicornia meyerana, Limonium scabrum, Disphyma crassifolium, Sporobulus virginicus, Senecio rosmarinifolius, Juncus kraussii, Atriplex vestita* and *Potamogeton pectinatus*. Of these *Sarcocornia perennis* is the dominant marcophyte. The marsh itself shows vertical zonation, four zones were recognised: a *Spartina* zone, *Sarcocornia* zone, *Chenolea* zone and a mixed zone (Taylor 1987). *Zostera capensis* beds and dense patches of the macroalga *Codium tenue* occurred over the entire length of the estuary and the authors estimated that the macrophytes contributed significantly to total system primary production.

The Kieskamma was an intermediate system with as erratic freshwater inflow. Salinites ranged from 0 to 35 ppt at the head and remained around 35 ppt at the mouth which was open at all times. Turbidity was extremely variable and high at times of freshwater input due to erosion in the catchment. Information is not available but it can be assumed that submerged macrophytes were virtually absent. Chlorophyll levels were intermediate between the Great Fish and Kariega estuaries, averaging 8.7 μg l^{-1}. Allanson and Read (1987) note that the high silt loads are inimical to benthic flora and fauna and that catchment restoration is a major priority if a diverse and productive estuarine biota is to be sustained.

In reviewing the findings on the three aforementioned estuaries, Allanson and Read (1987) conclude that minimal freshwater flow for up to 5 years create homogeneous, non-turbid and diverse systems, provided the mouth does not close. Occasional flooding is required to scour deposited silt and maintain the longevity of the system. Such floods are not detrimental to the flora and fauna as the species present are resilient to flooding.

The Wilderness coastal lakes

Estuaries, lagoons and lakes in the Wilderness area have been particularly well studied. Although the latter are not strictly estuarine, they are brackish and many of the processes which operate in them are applicable to more saline systems.

Groenvlei is a blind lake of variable water level and salinity. Martin (1959) gives considerable detail of the fen edaphic conditions and floral community and contrasts it with European equivalents. Emergent and submerged species found include *Cladium mariscus, Phragmites communis, Typha capensis, Naias, Scirpus littoralis, Chara* and *Potamogeton.*

Howard-Williams (1980) studied the three linked Wilderness lakes (Rondevlei, Langvlei, Eilandvlei), the interlinking channels and the Wilderness lagoon in considerable detail. All are shallow. Rondevlei, the most inland lake is nutrient rich with a maximum depth of 6 m. It is also the most saline of the lakes because, although it is not connected to the sea, it is furthest from the main source of freshwater, the Touws river. Langvlei, maximum depth of 4 m, lies between Rondevlei and Eilandvlei (maximum depth 6.5 m), into which flows the Touws and the Duiwe Rivers. Eilandvlei is linked to the Wilderness Lagoon, 2-3 m deep, which would open naturally to the sea if the water level rose sufficiently. However, in order to prevent the inundation of low lying developments, the mouth is mechanically opened annually. Water levels therefore seldom rise above the extreme high tide level.

The underlying sediments of the lakes are marine sand with low nitrogen and phosphorus contents. However, in the shallower areas beneath the emergent macrophytes, the organic content as well as the nitrogen and phosphorus contents are high. This build up of nutrients could result from i) continuous depletion of the lower sediments followed by surface deposition on death; ii) physical trapping of nutrient rich detritus from water flowing through the communities; and iii) nitrogen fixation. The higher organic content in sediment below the emergent macrophytes as opposed to that in the sediment below the submerged macrophytes is ascribed to the greater accumulation of detritus. This occurs as the emergent species have higher productivities and slower decomposition rates.

The distribution of macrophyte species in these lakes did not relate to the average water salinities for the period March-May 1979. The least saline area, 5 ppt (Wilderness Lagoon) had no *Typha latifolia* and no *Scirpus littoralis* although these are generally found in fresh or brackish water. In addition there was less *Chara globularis* and *Potamogeton pectinatus* (both fresh and brackish water species) in the less saline waters, whilst *Ruppia cirrhosa* and more salt tolerant species decreased from brackish to saline water. Howard-Williams (1980) deduced that the vegetation distribution is a function not only of the present, but also the past, environmental conditions. The Wilderness Lagoon is opened to the sea annually at which time salinities reach 35 ppt in the lagoon but the remainder of the system stays brackish. This intrusion of saline water presumably prevents colonization by *T. latifolia* and *S. littoralis* but does not affect the *Phragmites australis* which grows equally well in an adjacent freshwater system. This species has a wide range of ecotypes some of which are salt tolerant (Bjork 1967, Waisel and Rechav 1970, in Howard-Williams 1980).

Productivities (g dry mass m^{-2} y^{-1}) of the various macrophytes in the system were of the order: *Typha latifolia* > *Phragmites australis* > *Scirpus littoralis* > *Potamogeton pectinatus* > *Chara globularis* > *Ruppia cirrhosa*. In general, productivities were low compared to those for the same species in other systems. This is ascribed to the fluctuating and occasionally high salinities and possibly nutrient limitation.

Weisser and Howard-Williams'(1982) study of the long term changes in macrophytes in the same system, supported Howard-Williams (1980) conclusion that long-term salinities were more important than short term ones in determining macrophytes distributions. They also found that encroachment by emergent macrophytes (which disrupts recreational activities) was associated with dropping water levels while decreases in submerged macrophytes were related to increases in wave action and water turbidity. Lowered water levels also coincide with increased salinities and in 1975 *Potamogeton pectinatus* disappeared from Rondevlei when salinities increased to 22 ppt. At the same time benthic algal mats of Cyanophyta were present and the stranded emergent vegetation *(Typha latifolia, Scirpus littoralis, Juncus kraussii* and *Paspalum vaginatum)* started dying although *Phragmites australis* cover increased. *Juncus kraussii* appears also to dominate in some areas as a result of grazing pressure.

Between 1979 and 1981, the submerged aquatic macrophyte vegetation in the Wilderness lakes died back significantly (Weisser *et al.* 1992) but was found to recover between 1982 and 1983. Possible reasons for the die-back were a decrease in water transparency, high water level management policy, planktonic algal blooms, development of periphyton on submerged plants and uprooting of plants by wave action during strong winds (Weisser and Howard-Williams 1982). Weisser *et al.* (1992) concluded that the aquatic plant communities of the Wilderness lakes are highly variable on a spatial and temporal scale due to a complex interplay of environmental and biotic factors.

The Swartvlei is another brackish coastal lake which, together with the estuary which connects it to the sea, has been particularly well studied. Howard-Williams and Allanson (1978 and 1979) report that the major emergent macrophytes in the Swartvlei, which has salinities of typically 6 to 16 ppt, are *Typha latifolia, Scirpus littoralis* (1675 g m^{-2}) and *Phragmites australis* (1500 g m^{-2}). The major submerged macrophytes are *Chara sp.* (150 g m^{-2}), *Potamogeton pectinatus* (1950 g m^{-2}) which grows down to 2.6 m and provides shelter from wave action for the *Chara, Cladophora* (epiphytic) and *Enteromorpha.* Near the estuary inlet where salinities are higher (>20 ppt), the submerged vegetation is dominated by *Ruppia cirrhosa* (150 g m^{-2}) and *Zostera capensis.* During a long period of closure when salinities fell to about 4 ppt, Kariba weed (*Salvinia molesta)* encroached into Swartvlei. Otherwise when salinities drop below 16 ppt there is an increase in plant-eating birds and the disappearance of *Enteromorpha.*

Productivities (g C m^{-2} y^{-1}) of the major plant groups were of the order: *Chara mariscus* > *Potamogeton pectinatus* > *Phragmites australis* = *Scirpus littoralis* > adenate periphyton > epiphytic algae > phytoplankton. Because of their high productivities, *P. pectinatus* and *C. mariscus* (the two submerged macrophyte species), contribute 85% to the total production for the system while phytoplankton which cover 72% of the area only contribute 6%. Despite the high production, particularly of *Potamogeton* which was three times higher than predicted by Westlake (1963), there was no evidence of a build up of organic sediment in Swartvlei. This is ascribed to the rapid decomposition rates which were verified experimentally. Siltation due to imported material will also be low because incoming water has a low sediment load. That the productivity of these macrophytes is controlled by irradiance is evidenced by their depth distributions (the lower depth appears to be 5-10 % of surface irradiance) and the finding that encroachment occurred historically during dry periods when water clarity improved and regression occurred during rainy periods due to the humic laden freshwater input.

Howard-Williams and Allanson (1978 and 1979) conclude that regular (annual) opening of the Swartvlei estuary mouth has given the system a stability which is beneficial to fish migrations and the maintenance of the present vegetation and allows regularly flushing of nutrients and accumulated organic matter.

Liptrot (1978) and Howard-Williams and Liptrot (1980) describe the Swartvlei estuary. Water clarity in the Swartvlei estuary is higher than in Swartvlei due to dilution and precipitation of the humics (brought in by the rivers which arise in well-forested mountain slopes) by seawater. The estuary substratum, like that of the vlei, is recently deposited dune sand. The mouth of the estuary closes annually, usually in winter (July) and it is opened artificially, if necessary, in spring when water levels exceed extreme high tide levels. Thus the mouth is usually only closed for about 3 months of the year, generally in winter when the south-westerly winds cause longshore sand transport (Whitfield 1988).

When the mouth is open the salinity decreases up the system and from spring to neap tides. A substantial volume of water is retained in the estuary during the tidal cycle i.e. water in the middle reaches. During the spring tide and the days approaching, the incoming tide enters more rapidly than the outgoing tide and the estuary tends to fill up with water, to a maximum of 1.3 m above mean sea level. During the neap tide the reverse is true, and the lowest tidal level of 0.3m above msl occurs during these tides (Whitfield 1988). Water currents in the estuary have been measured at 1.5 $m.s^{-1}$.

When the mouth is closed the salinity in the system drops, the vlei gradually feeds the estuary and the water level rises. When the mouth is open salinities oscillate from 35 to 8 ppt in response to freshwater flows. The tidal amplitude is about 0.6 m.

The major primary producers are *Zostera capensis, Ruppia cirrhosa* and phytoplankton. Primary production is unaffected by mouth closure over a period of 4 months. However, closure for over a year resulted in the disappearance of the dense *Enteromorpha* mat. This could have been due to increased grazing by birds, particularly coot, or to the reduction in salinity to 16 ppt. Howard-Williams and Liptrot (1980) found that *Zostera capensis* was dominant nearer the mouth, where salinities were more frequently higher, and penetrated as far as the seawater does. *Ruppia cirrhosa* occurred along the entire estuary but was densest where the salinity fluctuated around 20 ppt. The horizontal zonation of *R. cirrhosa* appeared to be maintained by competition with *Z. capensis* at the saline end (35 ppt) and *P. pectinatus* and *C. mariscus* at the fresh (10 ppt) end. Vertically, it is found down to 0.4 m. *Z. capensis* grows below this but not in the main channel where water speeds at spring tides reach 1.4 m s^{-1}. *Potamogeton pectinatus* and *Chara mariscus* did not occur where salinities reached 35 ppt and were even absent where salinities sporadically exceeded 10 ppt. However, a period of several months at 16 ppt had no deleterious effect on this species. The macrophytes, particularly *Z. capensis* support dense epiphyte populations about 25% of the mass of the supporting leaf. Epiphytic species found included: *Lynbya, Enteromorpha* (which forms detached mats above the *Z. capensis* in winter) *Cladophora, Percursia, Cocconeis, Ectocarpus, Polysiphonia, Chondria* and *Hypnea*. The estuary also has marginal salt marshes which are flooded at spring high and when the mouth is closed. Species present at the time of the study were: *Sarcocornia natalensis, Salicornia meyerana*, the grasses *Paspalum vaginatum* and *Sporobolus virginicus*. *Juncus kraussi* was also present.

Whitfield (1989) found that the invertebrate community of the *Zostera* beds was distinct from the unvegetated areas. Although living *Zostera* was not an important food source for the invertebrates examined, preliminary analysis showed that most invertebrate species feed on detritus and dissolved microorganisms.

Bot River estuary

Like the Natal estuaries, many of the Cape estuaries become brackish when the mouth is closed and water levels rise. The effect of mouth closure and regular artificial opening has been particularly well studied in the Bot River estuary, where a multidisciplinary research project was carried out. Details of the findings which led to the conclusion that regular artificial opening of the mouth, every 3-4 years, is beneficial are given below.

According to Bally (1985) the Bot system consists of the Bot and the Kleinmond. The latter opens annually to the sea. The sand bar at the mouth of the former has been artificially opened every 3-5 years for the last century. The artificial opening being carried out in order to increase the salinity and allow the entry and survival of steenbras, leervis and elf which are valuable for commercial and recreational fishing. From his study of the present and past morphology of the dunes and the sand bar, Van Heerden (1985) concludes that closure of the mouth is the natural result of the high energy surf-zone and the unstabilized dunes in the area. It seems likely that natural opening has not been frequent for at least 300 years (Bally 1985). Between openings the salinity in the estuary drops and migrant, estuarine fish may die, despite their wide salinity tolerances (4 ppt to >35 ppt). Also between openings the reduced flow rates lead to increased siltation which renders the water and shores unsuitable for recreation and increased water levels erode banks and destroy development (Fromme 1985).

A quantitative study of the physical and chemical changes that occur as a result of opening was made by Bally and Mcquaid (1985). Between openings the water level rises to and remains at about 1.8 m above MSL, during which time salinities may drop to < 1 ppt. Generally salts decrease in concentration with time after closure, although this is not so for the biologically important nutrients (nitrogen, phosphorus and silica) which vary randomly. The system is rarely vertically stratified being 1-2 m deep in general and only 3.5 m deep in the channel. However, horizontal stratification does occur as a result of freshwater inflows at the upper end and seawater inputs over the bar at the lower end. Bally and Mcquaid (1985) conclude that with the present regime (opening every 3-5 years), the system is essentially estuarine with an average salinity of 20 ppt. Branch *et al.* (1985) conclude on the basis of the above literature that permanent closure of the mouth would result in a freshwater lake.

Bally *et al.* (1985) described the primary production of the Bot during a stable period when the mouth had been closed for 4 years. At this time the salinities were 8-16 ppt and water levels were high. *Phragmites australis* and *Scirpus littoralis* were present in the upper estuary, while *Ruppia maritima* dominated the submerged vegetation. *Potamogeton pectinatus* (down to 2.5 m), *Chara sp.* and *Cladophora sp.* were also present. The grass *Sporobolus virginicus* dominated areas which are occasionally flooded.

Contributions to the total primary production of the system were of the order: 72% by submerged macrophytes, 14% emergent reeds, 7% benthic diatoms, 7% phytoplankton. The importance of macrophytes was due, not only to their high productivities per unit area but also to their extensiveness. The productivity of *Potamogeton pectinatus* was highest with values double those obtained by Howard-Williams and Allamson (1978) in Swartvlei. The productivities of the other submerged macrophytes were also high in comparison to values for the same species in Europe and USA, while values for the emergent species were generally lower. Phytoplankton productivity was also low by comparison with most estuaries other than British estuaries and Swartvlei (South Africa).

The submerged macrophytes are thus clearly the major primary producers in this shallow system. The effects of changing water levels and salinities on these species are therefore a major consideration. Bally *et al.* (1985) point out that as water levels rise, flooding new areas, there would be a simultaneous process of shading the deeper area below 2.5 m. Thus formerly productive area would become too deep to support significant primary production. The speed with which water level increase takes place is critical. A slow rate of change would allow species to grow towards the surface and remain at least in partly lit depths while a rapid increase results in death and recovery must be from seed. On the other hand, if the beds have been completely destroyed, the rate of inundation would not be important as recovery must be from seed. Water level decreases as a result of opening the mouth are always rapid, usually a drop of 3 m within hours. This resulted in large areas of macrophytes being left stranded and dying. Following the opening of the mouth in October 1981 it was conservatively estimated that over 80% of the submerged macrophytes were left stranded. In addition macrophyte beds that had become established near the mouth were washed out to sea. Along with this, great reductions in the number of birds, particularly the herbivorous red-knobbed coots, were noted.

With the regime of periodic (3-4 y) opening of the mouth the Bot estuary supports a large bird population and a population of marine fish which is desirable for angling. It also allows the estuary to act as a nursery for these fish which enter as juveniles during opening. The period of closure then prevents the exit of these fish and thus a population of larger fish is maintained than would if the mouth were permanently open. Permanent closing of the mouth would result in a freshwater system and the death of the marine fish species (Bennett *et al.* 1985)

Roberts *et al.* (1985a,b) studied the bacteria of the system but found little in the way of ecological implications.

Palmiet River estuary

In contrast to the Bot estuary and the Wilderness estuaries, the mouth of the Palmiet estuary in the south west Cape is almost always naturally open due to scouring by high freshwater inputs during the winter rainy season. In spite of seasonal variations in river inflow, the Palmiet estuary exhibits a layered stratification throughout the year (Largier and Slinger 1991). Branch and Day (1984) found that the estuary is strongly stratified except at the mouth where salinities vary with the tidal cycle. Bottom layer salinities are in the range 31-35 ppt in summer and 20-35 ppt in winter. Surface waters range from 0-35 ppt in summer. In winter the salinity at the mouth drops, reducing the range.

During winter, water speeds are greatest during ebb tides. Speeds of 1.14 $m\ s^{-1}$ were measured during outflow in July but this is estimated to be half the maximum. Inflow during the flood tide at that time of year was 0.68 $m\ s^{-1}$. During summer, the situation was reversed and flood tide speeds (0.96 m s^{-1}) were greater than ebb tide speeds, but still lower than maximum winter speeds. Tidal exchange with the sea may be as much as 50% of the total volume at neap tides and flushing time in March is 2.5-6.0 days. Outflow at the mouth during winter is about 150% of the total volume of the estuary and flushing times may be as little as 24h.

The freshwater flowing into the system is darkly stained with humics but the sediment load is low. In April total particulate organic matter content of the water was higher during flood than ebb tides, reflecting higher levels in the seawater (38 mg l^{-1}) than in the river water (4 mg l^{-1}). Measured nutrient levels (phosphate, nitrate, ammonia and silicate) were in the range for estuaries given by Day (1981b).

Sediments are coarse, 65% gravel and 34% sand, increasing to 99% sand at the mouth. The mud fraction is insignificant throughout the estuary and organic content is low (< 0.6%). Sediments are transported close to the bottom and load correlates with water speed. Water speeds less than 0.75 m s^{-1} result in little or no movement of sand. Sand will therefore be imported during summer months when flood tide velocities are sufficient for transport.

The estuary supports virtually no attached macrophytes. Branch and Day (1984) found a *Cladophora* sp. present (132 g m^{-2}) over most of the estuary below the halocline, for a short period in summer, when flow was slow. *Enteromorpha* is usually present on rocky substrata near the mouth and there is a small salt marsh. They also found low chlorophyll-a concentrations both in the water column (2.1 - 8.4 μg l^{-1} in December and April 1.5 - 4.8 μg l^{-1}) and in the sediment (generally < 6 μg g^{-1} sediment, not exceeding 18 μg g^{-1} sediment). Imported detritus consisted of palmiet reed (*Prionum serratum*) from the river and kelp (*Ecklonia maxima*) from the sea. Calculations showed that allochthonous material (imports) exceeded autochthonous production by a factor of 3.6 (by mass).

According to Largier and Slinger (1991) an effective management policy for the Palmiet estuary would be an open mouth as this would ensure continual renewal of the long-residence bottom water and prevent the development of anoxic conditions.

Langebaan lagoon

Langebaan lagoon is completely marine except for a little freshwater seepage during the rainy winter period. It is tidal, exchanging half its water at each tide. As such it is strictly a bay, not an estuary, but it represents the type of system towards which an estuary, with severely reduced freshwater inputs but with an open mouth, would change. The abiotic conditions and vegetation of the lagoon as described by Christie (1981) are given below.

In 1981, Christie found the average depth of the lagoon was 1-2 m and the maximum 6 m. The sediment was marine sand, with the finer grades on the western side where water currents were weakest. Nitrate concentrations were higher towards the marine end of the lagoon while phosphate increases towards the inland end near the salt marshes. Nitrate concentrations near the mouth were highest in summer. Ranges for both these nutrients were low compared to most estuaries.

Phragmites australis and *Typha capensis* were found where there was freshwater seepage at the sheltered end of the lagoon. There was some salt marsh with the following species: *Sarcocornia perennis, Spartina maritima, Scirpus triqueter, Chenolea diffusa, Limmonium scabrum* and *Triglochin bulbosum.* These salt marsh species were most abundant at the sheltered end of the lagoon (away from the sea) where nutrients in the marsh water were highest and water speeds are lowest.

Zostera capensis occurred in the intertidal and on submerged sandbanks. It was concentrated at the closed end of the lagoon where there was seepage water and the sandbanks were flat. Standing crop was highest in sheltered areas. Maximum above ground standing crop was 226 g m^{-2} and productivity was assumed to be 3.8 times this (Sand-Jensen 1975). The productivities of *Phragmites, Typha, Sarcocornia* and *Spartina* were all similar, while *Scirpus* is about 4 times more productive per unit area. *Zostera* is only about a third as productive.

Gracilaria verrucosa was the dominant macrophyte. It occurred in the open lagoon towards the mouth, on sublittoral sand banks, although large areas were exposed at spring low tides. Maximum standing biomass was 543 g drymass m^{-2} in summer when nitrate concentrations were highest. *Gracilaria* productivity per unit area is slightly lower than that for *Spartina*.

Chlorophyll values were highest in summer and highest near the mouth of the lagoon. The maximum recorded level was 9.5 $\mu g\ l^{-1}$. Production values ranged from 32-314 mg C $m^{-3}\ d^{-1}$. Sediment chlorophyll-a values ranged from 0-34 $\mu g\ g^{-1}$ sediment and the maximum biomass value for benthic microalgae was 18.9 g m^{-2}. Production was higher in muddy substrata at the sheltered end of the lagoon than on the exposed sandy beach (Fielding *et al.* 1988).

It was estimated that macrophyte production contributed 55% of the total primary production by the system, the phytoplankton 23% and benthic microalgae 22% (Christie 1981).

Summary

The Natal estuaries are notably turbid due to erosion in the catchments and generally lacking in submerged macrophytes. Freshwater inputs are highly seasonal in this area and the mouths of the smaller estuaries usually close for part of the year. The improved water clarity and sediment stability associated with these conditions is associated with increases in submerged macrophyte biomass. Hypersaline conditions in these estuaries have not been reported.

The plant ecology of a number of Cape estuaries and brackish coastal lakes has been studied. As with the Natal estuaries, reduced flooding leads to mouth closure. However, freshwater inputs, even at minimum levels, have been such that, in most instances, the salinity of the system drops and water levels rise when the mouth is closed. As in Natal, the periods of low freshwater input are associated with improved water clarity and sediment stability and a consequent increase in the biomass of brackish water submerged macrophytes. Emergent macrophytes form a major component of the vegetation of these systems which are mostly shallow with gently sloping banks. These species encroach and die back as water levels drop and rise. Once established, emergent macrophyte populations are maintained unless physically removed by high water velocities when the mouth is breached, either naturally or manually. In the systems studied phytoplankton contribute less than 10% to total system primary production.

The Kromme and the Kariega estuaries in the east Cape are notable in that, despite minimal feshwater inputs, the mouths have remained open. As in the aforementioned systems, the consequent high water clarity and sediment stability allows the development of a high submerged macrophyte biomass. Because the freshwater inputs are such that euhaline conditions are maintained, the species present are marine or euhaline and the systems can be equated to lagoons. Published work on Langebaan lagoon indicates that macroalgae and seagrasses dominate such systems, although salt marsh species are also important. Phytoplankton were estimated to contribute 23% to total system primary production in this lagoon.

A relatively large east Cape system which has a moderate freshwater input and whose mouth remain open at all times, is the Great Fish. In contrast to the Kromme, it is a phytoplankton dominated system.

Notably lacking from the literature on South African estuaries is the effect of the development of hypersaline conditions which would be anticipated in a system with a closed mouth and a low freshwater input for a protracted period.

6. REFERENCES

ADAMS, J.B. and M.M.B. TALBOT. 1992. The influence of river impoundment on the estuarine seagrass *Zostera capensis* Setchell. *Botanica Marina 35*: 69-75.

ADAMS, J.B., W.T. KNOOP and G.C. BATE. 1992. The distribution of estuarine macrophytes in relation to freshwater. *Botanica Marina 35*: 215-226.

ADMIRAAL. W. 1977. Influence of light and temperature on the growth rate of estuarine benthic diatoms. *Marine Biology 39*: 1-9.

ADMIRAAL, W. and H. PELETIER. 1980. Influence of seasonal variations of temperature and light on the growth rate of cultures and natural populations of intertidal diatoms. *Marine Ecology Progress Series 2*: 35-43.

ALLANSON, B.R. and R.C. HART. 1975. The primary production of Lake Sibaya, Kwazulu, South Africa. *Vern. int. Verein. Limnol. 19*: 1425-1433.

ALLANSON, B.R. and G.H.L. READ. 1987. The response of estuaries along the south easter coast of southern Africa to marked variation in freshwater inflow. Internal Report. Institute for Freshwater Studies. Rhodes University, Grahamstown. 42pp.

AMSPOKER, M.C. and C.D. McINTIRE. 1978. Distribution of intertidal diatoms associated with sediments in Yaquina estuary, Oregon. *Journal of Phycology 14*: 387-395.

ANDERSON, M.R. and J. KALFF. 1986a. Nutrient limitation of *Myriophyllum spicatum* growth *in situ*. *Freshwater Biology 16*: 735-743.

ANDERSON, M.R. and J. KALFF. 1986b. Regulation of submerged aquatic plant distribution in a uniform area of a weedbed. *Journal of Ecology 74*: 953-961.

ANDERSON, M.R. and J. KALFF. 1988. Submerged aquatic macrophyte biomass in relation to sediment characteristics in ten temperate lakes. *Freshwater Biology 19*: 115-121.

BAILLIE, P.W. 1987. Diatom size distributions and community stratification in estuarine intertidal sediments. *Estuarine, Coastal and Shelf Science 25*: 193-309.

BALLS, H., B. MOSS and K. IRVINE. 1989. The loss of submerged plants with eutrophication I. Experimental design, water chemistry, aquatic plant and phytoplankton biomass in experiments carried out in ponds in the Norfolk Broadland. *Freshwater Biology 22*: 71-87.

BALLY, R. 1985. Historical records of the Bot River estuarine system. *Transactions of the Royal Society of Southern Africa 45*: 291-303.

BALLY, R. and C.D. McQUAID. 1985. The physical and chemical characteristics of the waters of the Bot river estuary, South Africa. *Transactions of the Royal Society of Southern Africa 45*: 317-331.

BALLY, R., C.D. McQUAID and S.M. PIERCE. 1985. Primary production of the Bot river estuary, South Africa. *Transactions of the Royal Society of Southern Africa 45*: 333-345.

BARKO, J.W. 1982. Influence of potassium source (sediment vs. open water) and sediment composition of the growth and nutrition of a submerged freshwater macrophyte (*Hydrilla verticillata* (L.f.) Royle). *Aquatic Botany 12*: 157-172.

BARKO, J.W. and R.M. SMART. 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology 67*: 1328-1340.

BEGG, G.W. 1978. The estuaries of Natal. Natal Town and Regional Planning. Main Series Report Vol. 41. 657 pp.

BEGG, G.W. 1984a. The estuaries of Natal Part II. Natal Town and Regional Planning. Main Series Report Vol. 55. 631 pp.

BEGG, G.W. 1984b. The comparative ecology of Natal's smaller estuaries. Natal Town and Regional Planning Report Vol. 62. 182 pp.

BENNET, B.A., K.C.D. HAMMAN, G.M. BRANCH and S.C. THORNE. 1985. Changes in the fish fauna of the Bot River estuary in relation to opening and closure of the estuary mouth. *Transactions of the Royal Society of Southern Africa 45*: 449-464.

BJöRK, S. 1967. Ecological investigations of *Phragmites communis*: Studies in theoretic and applied limnology. *Folia Limnologica Scandinavica 14*: 1-248.

BOLEN, E.G. 1964. Plant ecology of spring-fed salt marshes in Western Utah. *Ecological Monographs 34*: 143-165.

BRANCH, G.M., R. BALLY, B.A. BENNET, H.P. DE BECKER and G. FROMME. 1985.

Synopsis of the impact of artificially opening the mouth of the Bot river estuary: implications for management. *Transactions of the Royal Society of Southern Africa 45*: 465-483.

BRANCH, M. and G. BRANCH. 1985. *The Living Shores of Southern Africa*. C. Struik Pulishers, Cape Town. 272 pp.

BRANCH, G.M. and J.A. DAY. 1984. The ecology of South African estuaries. Part XIII. The Palmiet River estuary in the south-western cape. *South African Journal of Zoology 19*: 63-77.

BREEN, C.M., E.C. EVERSON and K. ROGERS. 1977. Ecological studies on *Sporobolus virginicus* (L.) Kunth with particular reference to salinity and inundation. *Hydrobiologia 54*: 135-140.

BURDICK, D.M., I.A. MENDELSSOHN and K.L. MCKEE. 1989. Live standing crop and metabolism of the salt marsh *Spartina patens* as related to edaphic factors in a brackish, mixed marsh community in Louisiana. *Estuaries 12*: 195-204.

CARRIKER, M.R. 1967. *In*: (G. Lauff, ed.) *Estuaries*. Am. Ass. Adv. Sci. Washington. 442 pp.

CARIGNAN, R. and J. KALFF. 1980. Phosphorus sources for aquatic weeds: water or sediments? *Science 207*: 987-989.

CHAMBERS, P.A. and J. KALFF. 1985. Depth distribution and biomass of submersed macrophyte communities in relation to Secchi depth. *Canadian Journal of Fisheries and Aquatic Sciences 42*: 701-709.

CHAPMAN, V.J. 1960. *Salt Marshes and Salt Deserts of the World*. Interscience Publishers, New York. 392 pp.

CHRISTIE, N.D. 1981. Primary production in Langebaan Lagoon. *In*: (J.H. Day, ed.) *Estuarine Ecology*. A.A. Balkema, Cape Town. pp: 101-115.

CLARK, J.R. 1977. *Coastal Ecosystem Management: A Technical Manual for the Conservation of Coastal Zone Resources*. Wiley, New York. 928 pp.

CLARKE, L.D. and N.J. HANNON. 1970. The mangrove swamps and salt marsh communities of the Sydney District. 3. Plant growth in relation to salinity and waterlogging. *Journal of Ecology 58*: 351-369.

COLIJN, F. and K.S. DIJKEMA. 1981. Species composition of benthic diatoms and distribution of chlorophyll-a on an intertidal flat in the Dutch Wadden Sea. *Marine Ecology Progress Series 4*: 9-21.

COLLINS, C.D., R.B. SHELDON and C.W. BOYLEN. 1987. Littoral zone macrophyte community structure: distribution and association of species along physical gradients in Lake George, New York, U.S.A. *Aquatic Botany 29*: 177-194.

CONGDON, R.A. and A.J. McCOMB. 1979. Productivity of *Ruppia*: Seasonal changes and dependence on light in an Australian estuary. *Aquatic Botany 6*: 121-132.

CONGDON, R.A. and A.J. McCOMB. 1981. The vegetation of the Blackwood River Estuary, south-west Australia. *Journal of Ecology 69*: 1-16.

CORRELL, D.L. 1978. Estuarine productivity. *BioScience 28*: 646-650.

DAEHNICK, A.E., M.J. SULLIVAN and C.A. MONCREIFF. 1992. Primary production of sand microflora in seagrass beds of Mississippi Sound. *Botanica Marina 35*: 131-139.

DAVIS, M.W. and C.D. McINTIRE. 1983. Effects of physical gradients on the production dynamics of sediment-associated algae. *Marine Ecology Progress Series 13*: 103-114.

DAY, J.H. 1981a. The estuarine flora. *In*: (J.H. Day, ed.) *Estuarine Ecology*. A.A. Balkema, Cape Town. pp: 147-178.

DAY, J.H. 1981b. Summaries of current knowledge of 43 estuaries in southern Africa. *In*: (J.H. Day, ed.) *Estuarine Ecology*. A.A. Balkema, Cape Town. pp: 251-330.

DAY, J.H. 1981c. Sediments, turbidity and light penetration. *In*: (J.H. Day, ed.) *Estuarine Ecology*. A.A. Balkema, Cape Town. pp 45-56.

deJONGE, V.N. 1985. The occurrence of "epipsammic" diatom populations : a result of interaction between physical sorting of sediment and certain properties of diatom species. *Estuarine, Coastal and Shelf Science 21*: 607-622.

DRINKWATER, K.F. 1986. On the role of freshwater outflow on coastal marine ecosystems - workshop summary. *In*: (S. Skreslet, ed.) *The Role of Freshwater Outflow in Coastal Marine Ecosystems*. NATO ASI Series, Vol. 67. Springer-Verlag, Berlin. pp: 429-438.

EDGECUMBE, D.J. 1980. Some preliminary observations on the submerged aquatic *Zostera capensis* Setchell. *South African Journal of Botany 46*: 53-66.

ERNST, W.H.O. 1990. Ecophysiology of plants in waterlogged and flooded environments. *Aquatic Botany 38*: 73-90.

FIELDING, P.J., K.St.J. DAMSTRA and G.M. BRANCH. 1988. Benthic diatom biomass, production and sediment chlorophyll in Langebaan Lagoon, South Africa. *Estuarine, Coastal and Shelf Science 27*: 413-426.

FIELDING, P.J., A.T. FORBES and N.T. DEMETRIADES. 1991. Chlorophyll concentrations and suspended particulate loads in St Lucia, a turbid estuary on the east coast of South Africa. *South African Journal of Marine Science 11*: 491-498.

FLINT, R.W. 1985. Long-term estuarine variability and associated biological response. *Estuaries 8*: 158-169.

FROMME, G.A.W. 1985. The hydrology of the Bot river estuary. *Transactions of the Royal Society of Southern Africa 45*: 305-315.

GALLAGHER, J.L. and F.C. DAIBER. 1974. Primary production of edaphic algal communities in a Delaware salt marsh. *Limnology and Oceanography 19*: 390-395.

GESSNER, F. AND W. SCHRAMM. 1972. Salinity and Plants. *In*: (O. Kinne, ed.) *Marine Ecology Volume 1, Part 2*. Wiley-Interscience, London. pp: 705-820.

GORDON, D.M., P.B. BIRCH and A.J. McCOMB. 1980. The effect of light, temperature and salinity on photosynthetic rates of an estuarine *Cladophora*. *Botanica Marina 13*: 749-755.

GRANT, J., U.V. BATHMANN and E.L. MILLS. 1986. The interaction between benthic diatom films and sediment transport. *Estuarine, Coastal and Shelf Science* 23: 225-238.

HALLER, W.T., D.L. SUTTON. and W.C. BARLOWE. 1974. Effects of salinity on growth of several aquatic macrophytes. *Ecology 55*: 891-894.

HANEKOM, N. and D. BAIRD. 1984. Fish communities and structures in *Zostera* and non-*Zostera* regions of the Kromme estuary, St. Francis Bay. *South African Journal of Zoology* 19: 295-301.

HANEKOM, N. and D. BAIRD. 1988. Distributions and variations in seasonal biomass of eelgrass *Zostera capensis* in the Kromme estuary, St Francis bay, South Africa. *South African Journal of Marine Science* 7: 51-59.

HARAMIS, G.M. and V. CARTER. 1983. Distribution of submersed aquatic macrophytes in the tidal Potomac river. *Aquatic Botany* 15: 65-79.

HARLIN, M.M. and B. THORNE-MILLER. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. *Marine Biology 65*: 221-229.

HART, R.C. and B.R. ALLANSON. Eds. 1984. Limnological criteria for management of water quality in the southern hemisphere. South African National Scientific Programmes Report No 93. CSIR, Pretoria. 181 pp.

HARWOOD, B.F. 1992. The benthic microalgal communities of small sandy beaches along the coastline of South Africa. Unpublished MSc dissertation, Botany Department, University of Port Elizabeth, South Africa. 124 pp.

HASLAM, S.M. 1971. Biological flora of the British Isles, *Phragmites communis* Trin. *Journal of Ecology 59*: 585-609.

HAW, P.M. 1984. Freshwater requirements of Knysna estuaries. School of Environmental Studies, University of Cape Town. Research Report No. 55.

HECHT, T. 1973. The ecology of the Kromme estuary with special refernce to *Sesarma catenata*. Unpublished MSc dissertation, Zoology Department, University of Port Elizabeth, South Africa. 150 pp.

HECKMAN, C.W. 1985. The development of vertical migration patterns in sediments of estuaries as a strategy for algae to resist drift with tidal currents. *Inst. Revue. Ges.*

Hydrobiol. 70: 151-164.

HEINSOHN, R.D. and A.B. CUNNINGHAM. 1991. Utilization and potential cultivation of the saltmarsh rush *Juncus kraussii*. *South African Journal of Botany 57*: 1-5.

HILMER, T. 1990. Factors influencing the estimation of primary production in small estuaries. Unpublished PhD thesis. Botany Department, University of Port Elizabeth, South Africa. 154 pp.

HILMER, T. and G.C. BATE. 1991. Vertical migration of a flagellate-dominated bloom in a shallow South African estuary. *Botanica Marina 34*: 113-121.

HO, Y.B. 1979. Shoot development and production studies of *Phragmites australis* (Cav.) Trin. ex Steudel in Scottish lochs. *Hydrobiologia 64*: 215-222.

HOCKING, P.J. 1989a. Seasonal dynamics of production, and nutrient accumulation and cycling by *Phragmites australis* (Cav.) Trin. ex Stuedel in a nutrient-enriched swamp in inland Australia. I. Whole plants. *Australian Journal of Marine and Freshwater Research 40*: 421-444.

HOCKING, P.J. 1989b. Seasonal dynamics of production, and nutrient accumulation and cycling by *Phragmites australis* (Cav.) Trin. ex Stuedel in a nutrient-enriched swamp in inland Australia. II. Individual shoots. *Australian Journal of Marine and Freshwater Research 40*: 445-464.

HOESE, H.D. 1967. Effects of higher than normal salinities on salt marshes. *Contributions in Marine Science University of Texas 12*: 249-261.

HOPKINS, J.T. 1964. A study of the diatoms of the Ouse estuary, Sussex. III. The seasonal variation in the littoral epiphyte flora and the shore plankton. *Journal of Marine Biology Association, U.K. 44*: 613-644.

HOPKINSON, C.S., J.G. GOSSELINK and R.T. PARRONDO. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. *Ecology 59*: 760-769.

HOWARD-WILLIAMS, C. and B.R. ALLANSON. 1978. Swartvlei Project Report, Part III. Community metabolism and phosphorus dynamics in the Swartvlei estuary. Rhodes

University, Institute for Freshwater Studies Special Report No. 78/4. 125 pp.

HOWARD-WILLIAMS, C. and B.R. ALLANSON. 1979. The ecology of Swartvlei: Research for planning and future management. Water Research Commission. 26 pp.

HOWARD-WILLIAMS, C. 1980. Aquatic macrophyte communities of the Wilderness lakes: community structure and associated environmental conditions. *Journal of the Limnological Society of Southern Africa 6*: 85-92.

HOWARD-WILLIAMS, C. and M.R.M. LIPTROT. 1980. Submerged macrophyte communities in a brackish South African estuarine-lake system. *Aquatic Botany 9*: 101-116.

HOWES, B.L., R.W. HOWARTH, J.M. TEAL AND I. VALIELA. 1981. Oxidation-reduction potentials in a salt marsh: Spatial patterns and interactions with primary production. *Limnology and Oceanography 26*: 350-360.

HUEBERT, D.B. and P.R. GORHAM. 1983. Biphasic mineral nutrition of the submersed aquatic macrophyte *Potamogeton pectinatus* L. *Aquatic Botany 16*: 269-284.

INGRAM, R.G., L. LEGENDRE, Y. SIMARD and S. LEPAGE. 1985. Phytoplankton response to freshwater runoff: the diversion of the Eastmain River, James Bay. *Canadian Journal of Fisheries and Aquatic Science 42*: 1216-1221.

JACKSON, M.D. and M.C. DREW. 1984. Effects of flooding on herbaceous plants. *In*: (T.T. Kozlowski, ed.) *Flooding and Plant Growth*. Academic Press, Inc. New York, London.

JACOBY, J.M. 1987. Alterations in periphyton characteristics due to grazing in a Cascade foothill stream. *Freshwater Biology 18*: 495-508.

JENNES, M.I. and G.C.A. DUINEVELD. 1985. Effects of tidal currents on chlorophyll-a content of sandy sediments in the southern North Sea. *Marine Ecology Progress Series 21*: 283-287.

JOHNSTON, C.S. 1971. Macroalgae and their environment. *Proceedings of the Royal Society of England (B) 71*: 195-207.

JOSSELYN, M.N. and J.A. WEST. 1985. The distribution and temporal dynamics of the estuarine macroalgal community of San Francisco Bay. *Hydrobiologia 129*: 139-152.

KARENTZ, D. and C.D. McINTIRE. 1977. Distribution of diatoms in the plankton of Yaquina estuary, Oregon. *Journal of Phycology 13*: 379-388.

KATOH, K. 1992. Correlation between cell density and dominant growth form of epilithic diatom assemblages. *Diatom Research 7*: 77-86.

KENNISH, M.J. 1986. Ecology of Estuaries. CRC Press, Inc. Florida, U.S.A. pp: 149-204.

KING, J., F. DE MOOR, A. BOTHA and A. COETZER. 1989. Water quantity requirements of invertebrates, macrophytes and other mesobiota. *In*: (A.A. Ferrar, ed). *Ecological Flow Requirements for South African Rivers*. S.A. National Scientific Programmes Report No. 162. pp: 57-70.

LARGIER, J.L. and J.H. SLINGER. 1991. Circulation in highly stratified southern African estuaries. *Southern African Journal of Aquatic Sciences 17*: 103-115.

LEE, V. and S. OLSEN. 1985. Eutrophication and management initiatives for the control of nutrient inputs to Rhode Island Coastal Lagoons. *Estuaries 8*: 191-202.

LINDBERG, S.E. and R. HARISS. 1973. Mechanisms controlling pore water salinities in a salt marsh. *Limnology and Oceanography 18*: 788-790.

LINTHURST, R.A. and E.D. SENECA. 1980. The effects of standing water and draingae potential on the *Spartina alterniflora* substrate complex in a North Carolina salt marsh. *Estuarine and Coastal Marine Science 11*: 41-52.

LINTHURST, R.A. and E.D. SENECA. 1981. Aeration, nitrogen and salinity as determinants of *Spartina alterniflora* Loisel. growth response. *Estuaries 4*: 53-63.

LIPTROT, M.R.M. 1978. Community metabolism and phosphorus dynamics in a seasonally closed South African estuary. MSc thesis, Rhodes University, Grahamstown. 130 pp.

LOBBAN, C.S. P.J. HARRISON and M.J. DUNCAN. 1985. Salinity. *In: The Physiological Ecology of Seaweeds*. Cambridge University Press, Cambridge. pp: 48-58.

LUBKE, R.A. 1988. The ecology of coastal regions. *In*: (R.A. Lubke, F.W. Gess and M.N. Bruton, eds.) *A Field Guide to the Eastern Cape*. The Grahamstown Centre of the Wildlife Society of Southern Africa, Grahamstown. pp: 317-371.

LUBKE, R.A. and Y. VAN WIJK. 1988. Estuarine plants. *In*: (R.A. Lubke, F.W. Gess and M.N. Bruton, eds.) *A Field Guide to the Eastern Cape*. The Grahamstown Centre of the Wildlife Society of Southern Africa, Grahamstown. pp: 133-145.

LUKATELICH, R.J. and A.J. McCOMB. 1986. Distribution and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. *Marine Ecology Progress Series 27*: 287-297.

LUKATELICH, R.J., N.J. SCHOFIELD and A.J. McCOMB. 1987. Nutrient loading and macrophyte growth in Wilson inlet, a bar-built South western Australian estuary. *Estuarine Coastal and Shelf Science 24*: 141-165.

MACNAE, W. 1957. The ecology of the plants and animals in the intertidal regions of the Zwartkops estuary near Port Elizabeth, South Africa. Parts 1 and 2. *Journal of Ecology 45*: 113-131 & 361-387.

MAIN, S.P. and C.D. McINTIRE. 1974. The distribution of epiphytic diatoms in Yaquina estuary, Oregon (U.S.A.). *Botanica Marina 17*: 88-99.

MALONE, T.C. 1977. Environmental regulation of phytoplankton productivity in the lower Hudson Estuary. *Estuarine and Coastal Marine Science 5*: 157-171.

MALONE, T.C., L.H. CROCKER, S.E. PIKE and B.W. WENDLER. 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Marine Ecology Progress Series 48*: 235-249.

MARTIN, A.R.H. 1959. The ecology of Groenvlei, A South African Fen. Part I. The Primary Communities. *Journal of Ecology 48*: 55-71.

MASON, C.F. and R.J. BRYANT. 1975. Production, nutrient content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L. *Journal of Ecology 63*: 71-95.

MASSON, H. and J.F.K. MARAIS. 1975. Stomach content analyses of Mullet from the Swartkops estuary. *Zoologica Africana 10*: 193-207.

McINTIRE, C.D. and W.S. OVERTON. 1971. Distributional patterns assemblages of attached diatoms from Yaquina estuary, Oregon. *Ecology 52*: 759-778.

McINTIRE, C.D. 1978. The distribution of estuarine diatoms along environmental gradients : a canonical correlation. *Estuarine and Coastal Marine Science 6*: 447-457.

McINTIRE, C.D. and M.C. AMSPOKER. 1986. Effects of sediment properties on benthic primary production in the Columbia River estuary. *Aquatic Botany 24*: 249-267.

McKEE, K.L. AND I.A. MENDELSSOHN. 1989. Response of a freshwater plant community to increased salinity and increased water level. *Aquatic Botany 34*: 301-316.

McKLUSKY, D.S. 1968. Some effects of salinity on the distribution and abundance of *Corophium volutator* in the Ythan estuary. *Journal of the Marine Biological Association, U.K. 48*: 443-454.

McMILLAN, C. and F.N. MOSELEY. 1967. Salinity tolerances of five marine spermatophytes of Redfish Bay, Texas. *Ecology 48*: 503-506.

McMILLAN, C. 1974. Salt tolerances of mangroves and submerged aquatic plants. *In:* (R.J. Reimold and W.H. Queen, eds.) *Ecology of Halophytes*. Academic Press Inc. New York and London. pp: 379-393.

McROY, C.C.P., R.J. BARSDATE and M. NEBERT. 1972. Phosphorus cycling in an eelgrass (*Zostera marina* L.) ecosystem. *Limnology and Oceonography 17*: 58-67.

MENDELSSOHN, I.A. and K.L. McKEE. 1988. *Spartina alterniflora* die-back in Louisiana: Time-course investigation of soil waterlogging effects. *Journal of Ecology 76*: 509-521.

MILLARD, N.A.H. and G.J. BROEKHUYSEN. 1970. The ecology of South African estuaries: Part 10: St Lucia: a second report. *Zoologica Africana 34*: 157-179.

MITCHELL, D.S. 1978. The potential for wastewater treatment by aquatic plants in Australia. *Water (Sydney) 5*: 15-17.

MITCHELL, S.F. 1989. Primary production in a shallow eutrophic lake dominated alternately by phytoplankton and by submerged macrophytes. *Aquatic Botany 33*: 101-110.

MOORE, W.W. and C.D. McINTIRE. 1977. Spatial and seasonal distribution of littoral diatoms in Yaquina estuary, Oregon (USA). *Botanica Marina 20*: 99-109.

MOSS, B. and H. BALLS. 1989. Phytoplankton distribution in a floodplain lake and river system II. Seasonal changes in the phytoplankton communities and their control by hydrology and nutrient availability. *Journal of Plankton Research 11*: 839-867.

MOSS, B., I. BOOKER, H. BALLS and K. MONSON. 1989. Phytoplankton distribution in a temperate floodplain lake and river systems I. Hydrology, nutrient sources and phytoplankton biomass. *Journal of Plankton Research 11*: 813-838.

MOUNTFORD, K. 1980. Aspects of the ecology of a small estuarine embayment. *Marine Biology 61*: 53-67.

NICHOLS, D.S. and D.R. KEENEY. 1976. Nitrogen nutrition of *Myriophyllum spicatum*: uptake and translocation of $_{15}$N by shoots and roots. *Freshwater Biology 6*: 145-154.

NIENHUIS, P.H. 1983. Temporal and spatial patterns of eelgrass (*Z. marina*) in a former estuary in the Netherlands dominated by human activities. *Mar. Tech. Sec. J. 17*: 69-77

NIXON, S.W. and C.A. OVIATT. 1973. Ecology of a New England salt marsh. *Ecological Monograph 43*: 463-498.

O'CALLAGHAN, M. 1987. Salt marshes along the Cape coast. *In: Ecology and Conservation of Wetlands in South Africa*. CSIR Ocassional Report No. 28.

ODUM, W.E. 1970. Insidious alteration of the estuarine environment. *Trans. Act. Am. Fish. Soc. 99*: 836-847.

OLFF, H., J.P. BAKKER and L.F.M. FRESCO. 1988. The effect of fluctuations in tidal

OLFF, H., J.P. BAKKER and L.F.M. FRESCO. 1988. The effect of fluctuations in tidal inundation frequency on a salt-marsh vegetation. *Vegetatio 78*: 13-19.

ORTH, R.J. 1977. Effect of nutrient enrichment on growth of the eelgrass *Zostera marina* in the Chesapeake Bay, Virginia, U.S.A. *Marine Biology 44*: 187-194.

PALMER, J.D. and F.E. ROUND. 1965. Persistent vertical-migration rhythms in benthic microflora. I. The effect of light and temperature on the rhythmic behaviour of *Euglena obstusa*. *Journal of Marine Biology Association, U.K. 45*: 567-582.

PEARCY, R.W. and S.L. USTIN. 1984. Effects of salinity on growth and photosynthesis of three California tidal marsh species. *Oecologia 62*: 68-73.

PETERSON, B.J. 1980. Aquatic primary productivity and the C^{14}-CO_2 method: A history of the productivity problem. *Ann. Rev. Ecol. Syst. 11*: 359-385.

PETERSON, D.H. and J.F. FESTA. 1984. Numerical simulation of phytoplankton productivity in partially mixed estuaries. *Estuarine, Coastal and Shelf Science 19*: 563-589.

PETERSON, C.G. 1987. Gut passage and insect grazer selectivity of lotic diatoms. *Freshwater Biology 18*: 455-460.

PHLEGER, C.F. 1971. Effect of salinity on growth of a salt marsh grass. *Ecology 52*: 908-911.

PRICE, J.S., K. EWING, M-K. WOO and K.A. KERSHAW. 1988. Vegetation patterns in James Bay coastal marshes. II. Effects of hydrology on salinity and vegetation. *Canadian Journal of Botany 66*: 2586-2594.

RAMM, A.E.L. 1990. Application of a community degradation index to 62 estuaries in southern Africa. *Water Research 22*: 293-301.

REDDERING, J.S.V. and K. ESTERHUYSEN. 1983. Research on sedimentation in estuaries. Sedimentation in the Kromme estuary. University of Port Elizabeth. *Rosie Report No. 6*. 92 pp.

REED, R.H. and G. RUSSELL. 1979. Adaptation to salinity stress in populations of *Enteromorpha intestinalis* (L.) Link. *Estuarine and Coastal Marine Science 8*: 251-258.

ROBERTS, C.H., G.M. BRANCH and F.T. ROBB. 1985a. The annual cycle of free-floating bacteria in the Bot river estuary. *Transactions of the Royal Society of Southern Africa 45*: 353-362.

ROBERTS, C.H., G.M. BRANCH and F.T. ROBB. 1985b. The effect of salinity and temperature variations on the bacterial populations in the Bot river estuary. *Transactions of the Royal Society of Southern Africa 45*: 347-352.

ROBINSON, K.I.M., P.J. GIBBS, J.B. BARCLAY and J.L. MAUY. 1983. Estuarine fauna and flora of Smiths Lake, New South Wales. *Proceedings of the Linnean Society New South Wales 107*: 19-34

ROEMER, S.C., K.D. HOAGLAND and J.R. ROSOWSKI. 1984. Development of a fresh water periphyton community as influenced by diatom mucilages. *Canadian Journal of Botany 62*: 1799-1813.

ROMAN, C.T., W.A. NIERING and R.S. WARREN. 1984. Salt marsh vegetation change in response to tidal restriction. *Environmental Management 8*: 141-150.

SAND-JENSEN, K. 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig. Denmark. *Ophelia 14*: 185-201.

SCHAFFER, G.P. 1988. K-systems analysis for determining the factors influencing benthic microfloral productivity in a Louisiana estuary, USA. *Marine Ecology Progress Series 43*: 43-54.

SCHELSKE, C.L. and E.P. ODUM. 1961. Mechanisms for maintaining high productivity in Georgia estuaries. *Proceedings of the Gulf Caribbean Fisheries Institute 14*: 75-80.

SCHLEYER, M.H. and G.A. ROBERTS. 1987. Detritus cycling in a shallow coastal lagoon in Natal, South Africa. *Journal of Experimental Marine Biology and Ecology 110*: 27-40.

SIMPSON, R.L., R.E. GOOD, M.A. LECK and D.F. WHIGHAM. 1983. The ecology of freshwater tidal wetlands. *BioScience 33*: 255-259.

SLOEY, W.E., F.L. SPANGLER and C.W. FETTER Jr. 1978. Management of freshwater wetlands for nutrient assimilation. *In*: (R.E. Good, D.F. Whigham and R.L. Simpson) *Freshwater Wetlands: Ecological Processes and Management Potential*. Academic Press. New York. pp: 321-340.

SMART, R.M. and J.M. BARKO. 1978. Influence of sediment salinity and nutrients on the physiological ecology of selected salt marsh species. *Estuarine and Coastal Marine Science 7*: 487-495.

SMETACEK, V.S. 1986. Impact of freshwater discharge on production and transfer of materials in the marine environment. *In*: (S. Skreslet, ed.) *The Role of Freshwater Outflow in Coastal Marine Ecosystems*. NATO ASI Series, Vol. 67. Springer-Verlag, Berlin. pp: 85-106.

STARFIELD, A.M., B.P. FARM and R.H. TAYLOR. 1989. A rule-based ecological model for the management of an estuarine lake. *Ecological Modelling 46*: 107-119.

STROSS, R.G. and R.C. SOKOL. 1989. Runoff and flocculation modify underwater light environment of the Hudson, River Estuary. *Estuarine, Coastal and Shelf Science 29*: 305-316.

SULLIVAN, M.J. 1975. Diatom communities from a Delaware salt marsh. *Journal of Phycology 11*: 384-390.

SUMNER W.T. and C.D. McINTIRE. 1982. Grazer-periphyton interactions in laboratory streams. *Archiv fur Hydrobiologie 93*: 135-157.

TALBOT, M.M.B., G.C. BATE and E.E. CAMPBELL. 1990a. A review of the ecology of surf-zone diatoms, with special reference to *Anaulus australis*. *Oceanogr. Mar. Biol. Annu. Rev. 28*: 155-175.

TALBOT, M.M.B., W.T. KNOOP and G.C. BATE. 1990b. The dynamics of estuarine macrophytes in relation to flood/siltation cycles. *Botanica Marina 33*: 159-164.

TAYLOR, D.I. 1987. Tidal exchanges of carbon, nitrogen and phosphorus between a *Sarcocornia* salt-marsh and the Kariega estuary, and the role of salt-marsh bracyura in this transfer. Unpublished PhD thesis. Rhodes University, Grahamstown, South Africa.

THERRIAULT, J.C. and M. LEVASSEUR. 1986. Freshwater runoff control of the spatio-temporal distribution of phytoplankton in the lower St. Lawrence estuary (Canada). *In*: (S. Skreslet, ed.) *The Role of Freshwater Outflow in Coastal Marine Ecosystems*. NATO ASI Series, Vol. 67. Springer-Verlag, Berlin. pp: 251-260.

TOETZ, D.W. 1974. Uptake and translocation of ammonia by freshwater hydrophytes. *Ecology 55*: 199-201.

UNGAR, I.A. 1962. Influence of salinity on seed germination in succulent halophytes. *Ecology 43*: 763-764.

VAN HEERDEN, I. 1985. Barrier/estuarine processes, Bot River estuary - an interpretation of aerial photographs. *Transactions of the Royal Society of Southern Africa 45*: 239-251.

VARELA, M. 1985. Medida de la produccion primaria de la microflora bentonica. Revision metodologica. *Boletin del Instituto Espanol de Oceanografia* 2: 58-68.

VEGTER, F. 1977. The closure of the Grevelingen estuary, its influence on phytoplankton primary production and nutrient content. *Hydrobiologia 51*: 67-71

VERHOEVEN, J.T.A. 1975. *Ruppia*-dominated communities in the Camargue, France. Distribution and structure in relation to salinity and salinity fluctuations. *Aquatic Botany 1*: 217-241.

WARD, C.J. 1976. Aspects of the ecology and distribution of submerged macrophytes and shoreline vegetation of Lake St. Lucia. *In:* (A.E.F. Heydorn ed.) *St Lucia Scientific Advisory Council workshop* - Charters Creek, February 1976. Natal Parks Board, Pietermaritzburg.

WASELL, A. and H. HÅKANSSON. 1992. Diatom stratigraphy in a lake on Horseshoe Island, Antartica : a marine-brackish-fresh water transition with comments on the systematics and ecology of the most common diatoms. *Diatom Research 7*: 157-194.

WEISSER, P.J. and C. HOWARD-WILLIAMS. 1982. The vegetation of the Wilderness Lakes system and the macrophyte encroachment problem. *Bontebok 2*: 19-40.

WEISSER, P.J., A.K. WHITFIELD and C.M. HALL. 1992. The recovery and dynamics of submerged aquatic macrophyte vegetation in the Wilderness lakes, southern Cape. *Bothalia 22*: 283-288.

WESTLAKE, D.F. 1963. Comparisons of plant productivity. *Biological Review 38*: 385-425.

WHITFIELD, A.K. 1988. The role of tides in redistributing macrodetrital aggregates within the Swartvlei estuary. *Estuaries 11*: 152-159.

WHITFIELD, A.K. 1989. The benthic invertebrate community of a southern Cape estuary: structure and possible food sources. *Transactions of the Royal Society of South Africa 47*: 159-179.

WILSEY, B.J., K.L. MCKEE and I.A. MENDELSSOHN. 1992. Effects of increased elevation and macro- and micronutrient additions on *Spartina alterniflora* transplant sucess in salt-marsh dieback areas in Louisiana. *Environmental Management 16*: 505-511.

YOUNT, J.R. and T.V. BELANGER. 1988. Population trends in the phytoplankton and zooplankton of the upper and middle St. Johns River, Florida, 1983-1984. *Florida Science 51*: 76-85.

ZEDLER, J.B. 1980. Algal mat productivity comparisons in a salt marsh. *Estuaries 3*: 122-131.

ZEDLER, J.B. 1983. Freshwater impacts in normally hypersaline marshes. *Estuaries 6*: 346-355.